How is the age of an anthropogenic habitat - calcareous grasslands - affecting the occurrence of plant species and vegetation composition - a historical, vegetation and habitat ecological analysis

Welche Bedeutung hat das Alter eines anthropogenen Lebensraums, der Kalkmagerrasen, für das Vorkommen von Pflanzenarten und die Zusammensetzung der Vegetation - eine kulturhistorische, vegetations- und standortökologische Analyse.

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Chapter 1

General introduction

Dry grasslands – an extraordinary habitat

When we evaluate natural habitats, we often ask why they are valuable from a conservation point of view. Oftentimes we evaluate their species diversity. For individual species, we consider whether they are original or not. This, of course, raises the question of exactly what the word "original" means. If we are looking for an answer to the issue of originality, we need to look at how old a habitat is.

If we ask this question in Central Europe, we find a fascinating biotope - dry grasslands. For several thousand years, they were necessary for humans as a place of grazing livestock. On the vast majority of their size, grasslands are conditioned by man, without whose activity they would disappear. Yet the grasslands may be extremely old because they follow on, in general, the old-holocene vegetation. So, they may be a more ancient biotope than common forests with beech and fir. Furhtermore, dry grasslands are exceptionally species-rich.

The present dissertation is a modest contribution to understand this fascinating biotope and asks questions related to how different historical factors affect the state of the current vegetation.

History of dry grasslands and species diversity

Dry calcareous grasslands may strongly differ in their floristic composition, which may depend not only on present day habitat quality and management, either by grazing or by mowing, but also on their age (Gradmann 1933). Relict grasslands may exist in direct continuity with post glacial cold continental steppes but have been maintained by humans since the beginning of settlement (Gradmann 1933, Pokorný 2005, Ložek 2007, Pokorný et al. 2015). In contrast, semi-natural grasslands, which are the object of the present dissertation, developped mainly as a consequence of forest grazing as secondary vegetation. These grasslands have provably existed since the Neolithic Age (Kaligarič et al. 2006, Dutoit et al. 2009, Poschlod & Baumann 2010, Hájková et al. 2011, Hájek et al. 2016, Robin et al. 2018).

Species, which later constituted species pool of the semi-natural grasslands may have survived either in open forests (Roleček et al. 2014, Hájek et al. 2016) or in microrefugia such as small patches on rocky outcrops (Bylebyl et al. 2008, Ložek 2011, Tausch et al. 2017). Based on extensive review, Kajtoch et al. (2016) are showing that distinctiveness of many dry grassland species populations suggests a survival in the Central Europe during glacial maxima. Surviving of heliophilous species throughout the Holocene was surely supported due to grazing by wild animals (Vera 2000). Many species, however, have probably only immigrated into Central Europe with the first settlers and their livestock (Poschlod 2015b, Meindl et al. 2016, Leipold et al. 2017).

Representation of relict species of primary grasslands increases with the continentality level of particular region. A typical example of a significantly continental territory in Central Europe is the Böhmisches Mittelgebirge in north-west Bohemia, the Saale-Unstrut Region in central Germany, the banks of the river Oder and Pannonikum (Ellenberg 2010). To the subcontinental regions can be included Franconian Alb near Regensburg (Poschlod et al. 2016) or Bohemian Karst in central Bohemia (Ložek et al. 2005, Ložek 2007). Present dissertation deals with the two last regions.

Loss of area, nature conservation and management

Dry calcareous grasslands are, due to their high species diversity and the occurrence of many relic species, regarded as one of the most important habitats in Europe from a conservation point of view (e.g. Korneck et al. 1998, Wallis de Vries et al. 2002, Sádlo et al. 2007). They are in the focus of conservation efforts and are listed in the Annex I of the Natura 2000 Habitats Directive (92/43/EEC).

To understand the threat of dry calcareous grasslands, it is necessary to know the historical dynamics of their area. Dry grassland extended their area in connection with the landscape colonization by man. Important periods of extension were Bronze Age and especially the High Medieval Ages and then the 18th and 19th century of Modern Times (Baumann 2006, Poschlod & Baumann 2010). Because of low productivity and fundamental changes in agriculture came since the end of the 19th century to continual decrease of area (Quinger et al. 1994) with the strongest decline during the 1960s and 1970s (Mattern et al. 1992, Mauk 2005). Fundamental cause was increased imports of sheep wool from e.g., Australia and New Zealand, which resulted in a decline in sheep numbers (Poschlod & Wallis de Vries 2002, Baumann et al. 2005). Huge areas of dry grasslands were spontaneous overgrown by shrubs or were intentionally afforested (Fig. 1.1 – 1.6). In other places land use was intensified or buildings were constructed (Fig. 1.1 and 1.2). Numerous localities of high conservation value were lost.

Due to the loss of area, strong efforts exist to restore at least part of these localities (Bylebyl 2007, Calaciura & Spinelli 2008, Dostálek & Frantík 2008, Piqueray et al. 2011, Rákosy & Schmitt 2011, Piqueray et al. 2015). Most frequent management treatments are cutting of trees and shrubs, grazing, mowing, less often disturbance, e.g. by tanks, or burning (Bylebyl 2007). In order to be able to propose the most appropriate and effective treatments, we need to know the results of long-term experiments. An excellent case of great significance for planning in nature conservation are the grassland management experiments in the southwestern Germany (Baden-Württemberg) started in 1975 (Moog et al 2002, Römermann et al. 2009, Schreiber et al. 2009, Poschlod et al. 2011). Furthermore, a number of regional studies allow them to be evaluate by meta-analysis approach in order to find an optimal management regime and to compare, for example, the impact of pasture versus annual mowing on biodiversity (Tälle et al. 2016, 2018).

Fig. 1.1. and 1.2. – View from Strobelberg/Gänsleiten towards the castle in Kallmünz. The first photo comes from around 1920 (private archive Baptist Lell) and shows a varied landscape utilization including goose grazing on calcareous grasslands. The present state (photo taken by P. Karlík in spring 2009) is typical of the extension of the built-up area, intensive farming using machinery on well accesible places (in foreground) and the expansion of woods on less favourable places (in the background).

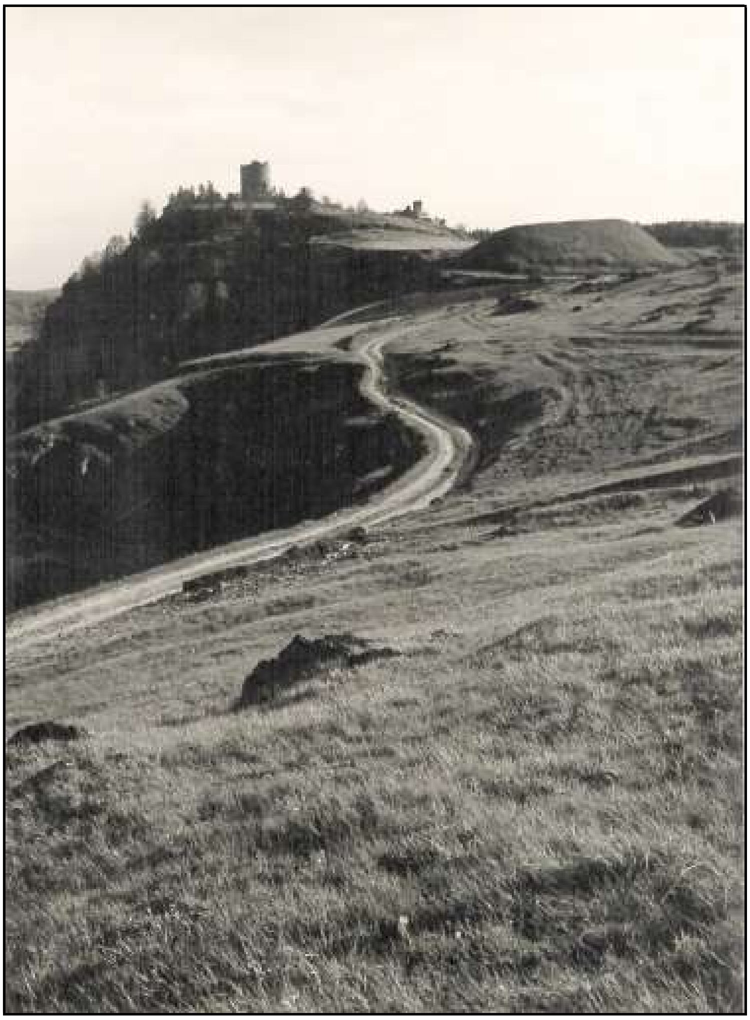

Fig. 1.3. and 1.4. – The old photo of Kallmünz castle on the Schloßberg shows a rather tree- and shrubless landscape with some woody plants restricted on close surroundings of the castle (photo taken by Baptist Lell in the year 1950). The spontaneous expansion of woods and tree plantation is visible on recent picture taken by P. Karlík in early spring 2008.

Fig. 1.5. and 1.6. – In foreground is locality „Hutberg bei Krachenhausen“. This site is today a nature protected area and is managed by sheep grazing, but the intensity of the pasture is noticeably lower than before. The current image shows higher sward and juniper shrubs. The expansion of woods is visible on recently not managed slopes in backgrounds. The old photo comes from around 1930 (archive Verlag Lassleben). The present state was documented by P. Karlík in early spring 2008.

Emergence of new grasslands, definition of ancient and recent grasslands

However, the process of land-use change is not trivial and unidirectional, because in addition to decline, many areas have also emerged. Thanks to the current evaluation of old maps in the GIS environment, we have a number of regional studies providing accurate data (Mailänder 2005, Baumann 2006, Johansson et al. 2008, Poschlod et al. 2016).

New grasslands established on cultivated land, i.e. on arable fields or vineyards. Especially after the wine-pest (phylloxera, *Daktulosphaira vitifoliae*) epidemic in the 19th century grasslands replaced abandoned vineyards (Hard 1964, Illyes & Boloni 2007). New grasslands either results from spontaneous succession or were artificially established by sowing hayseed (Hard 1964).

The process of grassland creation enhanced from the middle of the 19th century when new agricultural techniques were introduced, resulting in increased production (Hard 1964, Baumann et al. 2005, Mailänder 2005). Arable farming on marginal land was further abandoned because of socio-economic and political changes. An important role played the gradual decrease in the importance of self-sufficiency, related to the improvement of transport and the industrialization of rural areas. Large areas of new semi-natural grasslands developed in numerous regions in Central Europe only around the middle and in the second half of the 20th century on less agriculturally favourable land (Osbornová et al. 1990, Mailänder 2005, Chýlová & Münzbergová 2008, Poschlod et al. 2008). In post-communist countries was increase during 90ties especially significant (Ruprecht 2005, Illyés & Bölöni 2007, Lipský 2010, ČÚZK 2017).

Therefore, we may differentiate ancient and recent calcareous grasslands.We define ancient grasslands as those that are at least 180 years old and recent grasslands as those that are marked as arable fields at least on the first detailed maps published at the beginning of the 19th century of the Central European landscape (first cadaster maps available from 1820s and 1830s) or on someyounger maps (Mailänder 2005, Baumann 2006, Poschlod et al. 2008). An example of the distribution of ancient and recent grasslands in the Kallmünz region is shown on the Fig. 1.7.

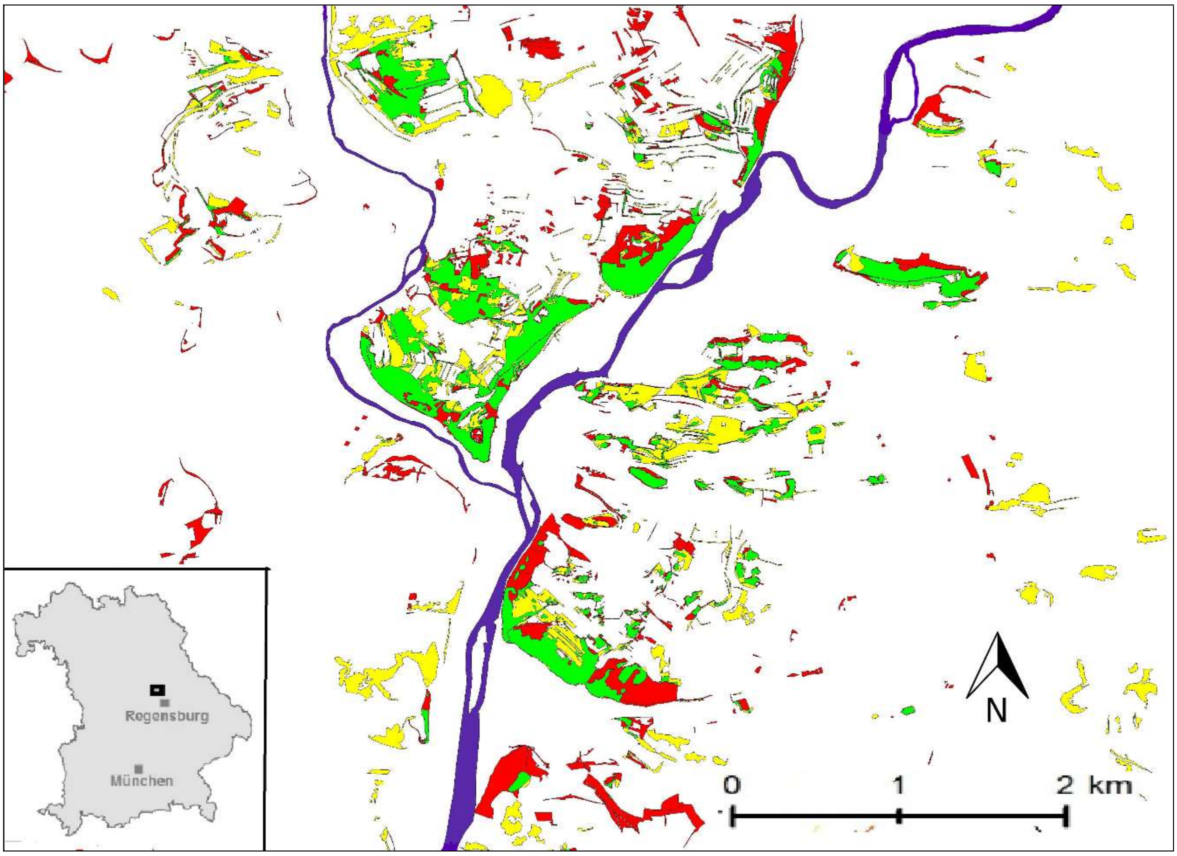

Fig. 1.7. – Changes in the distribution and status of calcareous grasslands in the surroundings of Kallmünz from 1830 to 1990. The ancient grasslands (continuous at least since 1830) are marked with green collor, recent grasslands (arisen between 1830-1990) are marked with yellow collor and grasslands lost between 1830-1990 are red. The map was created by intersection a layer of pastures ("Ödungen") from the cadastre map of the 30ies of the 19th century with a layer of semi-natural dry grassland habitat on calcareous substrates biotopes surveyed in 1990. (Accordings to Blattner 2004 and Baumann 2006).

Overall, the presented dissertation deals with three territories in detail, all of which are famous and very valuable Natura 2000 sites (Fig. 1.8). For all three areas there is a typical mosaic of well-preserved ancient grasslands and recent grasslands of different age. There are differences in history (past management practices), topography, partly geology but the most important is climate. These regions lie along a subocenaic to subcontinental climatic gradient; in the west the rather humid Kaltes Feld, in the middle the somewhat drier Kallmünz and in the -east the sub-continental Srbsko in the Bohemian Karst (Fig. 1.8).

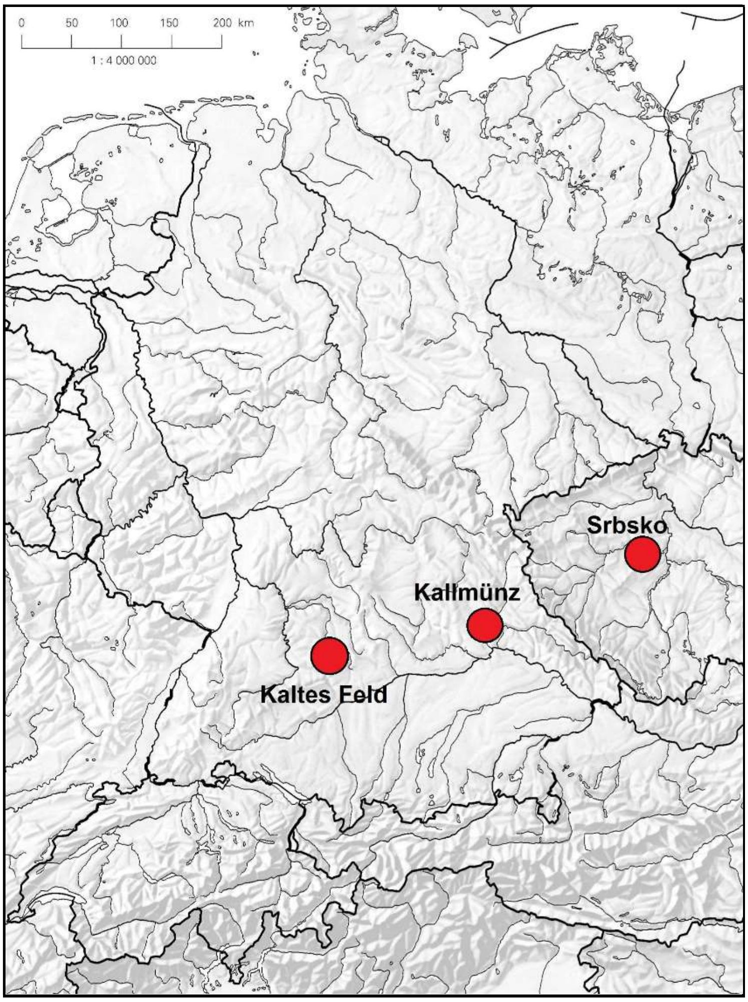

Fig. 1.8. – Geographical position of the three surveyed regions in the Central Europe.

Thesis outline

The objective of this thesis is to investigate the ecological differences between ancient and recent grasslands and try to explain the causes of these differences. The differences can be observed in many parameters, in aboveground flora and vegetation, in the composition and the size of soil seed bank and in soil chemical and physical properties. The results can be presented e.g. using indicator species or can be generalised using plant traits.

The breadth of topic that is adressed requires the use of a variety of methods. In the present study, classical field work, i.e. sampling of vegetation relevés or simple surveying of target species was supplemented by experiments in the greenhouse for the purpose to assess the seed bank and soil chemical and physical analyses. Due to the use of different map sources and the need to achieve high accuracy in site localization, it was necessary to work in a GIS environment.

The research presented in chapter 2 (**History or abiotic filter: which is more important in determining the species composition of calcareous grasslands?**) was conducted in the nature reserve “Kaltes Feld” located in the central part of the Jurassic mountains, in the so called Swabian Alb (southwestern Germany). I recorded there vegetation data from ten ancient and 12 recent grasslands. Some recent grasslands reached considerable age of 150 years. Furthermore, I pinpointed a broad set of environmental variables. I analysed data using both, univariate and multivariate statistical methods and I defined indicator species for ancient and recent grasslands fot the region of Kaltes Feld.

In chapter 3 (**Identifying plant and environmental indicators of ancient and recent calcareous grasslands**) I made analogical survey in another part of the Jurassic mountains, on the Franconian Alb near the small town Kallmünz (Bavaria, south Germany). The inclusion of this additional territory is a necessary step in deciding the extent to which the results, in particular the indicator species, can be generalized.

In next two chapters (chapter 4 and 5) I focused on the soil seed bank. I assessed composition and size of the seed banks using emergence method and compared it with aboveground vegetation to find out if there are still species indicating the former arable field use in recent grasslands.

In chapter 4 (**Soil seed bank composition reveals the land-use history of calcareous grasslands**) I investigated the soil seed banks in the two regions of the Jurassic mountains, where I already explored aboveground vegetation (see chapter 2 and 3).

In chapter 5 (**Soil seed banks and aboveground vegetation of a dry grassland in the Bohemian Karst**) I explored one region in the Bohemian Karst and thus I reached the climatic gradient of three regions, the rather humid Kaltes Feld, the somewhat drier Kallmünz and the sub-continental Srbsko in the Bohemian Karst.

Finally, the results of the previous chapters were reviewed with regard to their implications for nature conservation and restoration practice (chapter 6: **Perspectives of using knowledge about the history of grasslands in the nature conservation and restoration practice**).

Chapter 2

History or abiotic filter: which is more important in determining the species composition of calcareous grasslands?

Abstract

Dry calcareous grasslands belong to the most species-rich but also strongly endangered ecosystems of central Europe. Despite the dramatic loss of grasslands in the second half of the 20th century due to abandonment of land use or afforestation, also new grasslands have developed on former arable land. The main object of our study was to assess the effect of age on the vegetation and habitat properties of calcareous grasslands. We found that history (former land-use, age of habitats) of grassland localities is a fundamental attribute to both species composition of vegetation and habitat properties. Significant differences were found, especially in soil reaction and water-holding capacity. Therefore, we can state that both history and habitat properties determine the recent species composition pattern. Consequently, it was possible to identify species indicating the historical status of the grasslands. Indicators for ancient grassland (i.e., patches continuously used as pastures at least since 1830) could be assigned to typical *Festuco-Brometea* species but also more widespread grassland species such as *Carex flacca, Buphthalmum salicifolium, Carlina vulgaris, Cirsium acaule, Hippocrepis comosa* and *Scabiosa columbaria*. Indicators for recent grasslands (i.e. patches temporarily farmed as arable fields after 1830) belong to different phytosociological classes as *Festuco-Brometea* but also *Molinio-Arrhenatheretea, Trifolio-Geranietea sanguinei* and *Secalietea cerealis*. *Festuco-Brometea* species restricted to recent grasslands were e.g. *Thymus pulegioides* subsp. *carniolicus, Stachys alpina*, *Rhinanthus alectorolophus* and *Onobrychis viciifolia*.

The two latter species are survivors from the former arable cultivation, the first was an arable weed and the second a widespread fodder plant, but are now considered to be characteristic species of calcareous grasslands. Therefore, we claim that the occurrence of these species indicate calcareous grasslands that were previously arable fields and that recent grasslands are a monument to historical land use. Rare and/or endangered species were not only found in ancient but also in recent grasslands. Furthermore, recent grasslands have a high species diversity. Thus both, ancient and recent calcareous grasslands should be considered equally valuable from a nature-conservation point of view.

Keywords: ancient grasslands, biodiversity, calcareous grasslands, Central Europe, historical ecology, historical land use indicators, recent grasslands, Swabian Alb

Introduction

Calcareous grasslands belong mostly to the so-called semi-natural grasslands influenced and formed by husbandry. Their existence dates back at least to the Neolithic (Dutoit et al. 2009) or Bronze Age (Körber-Grohne & Wilmanns 1977, Thorley 1981, Ložek 1988, Ložek & Cílek 1995, Wilmanns 1997, Baumann & Poschlod 2008, Poschlod & Baumann 2010). Before the Neolithic Age dry grassland species were restricted to small scale patches like rock outcrops although in some more continental regions of Central Europe dry grasslands might have been formed from still existing steppic vegetation due to early colonization and continuous settlement (Gradmann 1933, Pokorný 2005, Ložek 2007).

Furthermore, some non-forest species currently occuring in dry grasslands might have survived there throughout the Holocene due to grazing by wild animals (Vera 2000). Periods of dry grassland extension started probably in the Bronze Age but also the Roman Age and especially the High and Late Medieval Ages and the 18th and 19th century of Modern Times (Baumann 2006, Poschlod & Baumann 2010). The decrease started at the end of the 19th century (Quinger et al. 1994) having the strongest decline during the 1960s and 1970s (Mattern et al. 1980, 1992, Mauk 2005) due to altered farming practices as well as by increased imports of sheep wool from e.g., Australia and New Zealand which resulted in decline of sheep numbers (Poschlod & Wallis de Vries 2002). Since calcareous grasslands also belong to the most species-rich habitats in central Europe (Korneck et al. 1998, Wallis de Vries et al. 2002, Sádlo et al. 2007) they are now in the focus of conservation efforts and are listed in the Annex I of the Natura 2000 Habitats Directive (92/43/EEC).

However, also new grasslands have developed from former arable fields since mid of the 19th century when agricultural techniques have improved (Hard 1964, Baumann et al. 2005, Mailänder 2005). Furthermore, after the wine-pest (*Phylloxera*) epidemy in the 19th century new grasslands have established on abandoned vineyards (Illyés & Bölöni 2007). Hard (1964) even states that they were artificially sown applying hayseed. A large proportion of recent grasslands has also developed in the middle and second half of 20th century in numerous regions in central Europe on less agricultural favourable sites when arable farming was abandoned because of socio-economical and political changes (Osbornová et al. 1990, Ruprecht 2005, 2006, Illyés & Bölöni 2007, Poschlod et al. 2008). Therefore, we may differentiate ancient and recent calcareous grasslands. We define ancient grasslands as those that are at least 180 years old and recent grasslands as those that are marked as arable fields at least on the first detailed maps published at the beginning of the 19th century of the Central European landscape (first cadaster maps available from 1820s and 1830s) or on some younger maps (Mailänder 2005, Baumann 2006, Poschlod et al. 2008).

The effect of habitat continuity on species richness and composition and habitat properties is recorded for forests (Peterken 1974, 1976, Peterken & Game 1981, 1984, Kubíková 1986, Koerner et al. 1997, Graae & Sunde 2000, Bellemare et al. 2002, Jacquemyn et al. 2003, Verheyen et al. 2003, Vojta 2007). A comparison of studies from different parts of Europe revealed a set of indicator species for ancient and recent forests (Wulf&Kelm 1994). The absence of ancient forest indicators in recent forests is attributed to either their dispersal limitation (Ehrlén & Eriksson 2000, Graae & Sunde 2000) or the lack of dispersal processes in the current landscape (Poschlod & Bonn 1998).

Until now, only few comparisons of ancient and recent grasslands exist which are related to species composition as well as habitat properties and identifying indicator species (Ejrnæs & Bruun 1995, Chýlová & Münzbergová 2008, Poschlod et al. 2008). There are however some studies related to populations of single species (Geertsema et al. 2002, Becker 2003, Herben et al. 2006) and species diversity (Austrheim et al. 1999, Bruun 2000, Bruun et al. 2001, Gustavsson et al. 2007, Pärtel et al. 2007, Waesch & Becker 2009). Other studies are related to the establishment of grasslands after abandonment of arable fields and restoration of afforested grasslands. Succession on former arable land to grasslands was described e.g., by Knapp (1979), Schmidt (1981), Soukupová (1984), Osbornová et al. (1990) and Ruprecht (2005, 2006). Gibson & Brown (1991), Verhagen et al. (2001), Pywell et al. (2002) and Kiehl & Pfadenhauer (2007) studied the establishment of grasslands on former arable fields after restoration management. Von Blanckenhagen & Poschlod (2005) investigated the re-establishment of calcareous grasslands after clear-cutting afforestations. Hirst et al. (2005) reported about the resilience of calcareous grasslands in military training areas after disturbance by military vehicles.

Like in recent forests, dispersal potential of the respective species both in space and time has been shown limiting species composition after reestablishment or restoration (Hutchings & Booth 1996). Grazing of domestic livestock was shown being the key factor in the dispersal of grassland species (Fischer et al. 1996, Stender et al 1997, Cosyns et al. 2005, Bugla 2008). Wells et al. (1976), therefore, stressed also time period after abandonment of arable fields being another key factor in the re-establishment of grasslands.

Summarizing, we can conclude that there is a lack in studies concerning how land use history affected species composition and habitat properties in grasslands. The following questions are addressed in the present paper: (i) What are the differences among ancient and recent calcareous grasslands regarding species richness and composition, selected physical and chemical soil properties? (ii) If there are any differences in vegetation are they caused either by the variable „land use history“ or by environmental variables or by both? (iii) Are there any plant-indicators for ancient and recent grasslands?

Material and methods

Study area

The study was carried out in the nature reserve "Kaltes Feld" located in the central part of the Jurassic mountains Swabian Alb in southwestern Germany (Fig. 2.1). Altitude ranges from 650 to 781m above sea level. The climate is temperate, with mean annual precipitation of 1050 mm and a mean annual temperature of 7°C (DW 1979). Geological substrate consists of Jurassic bedrock (Malm) containing hard and soft layers resulting in a relief of steep slopes around a plateau (LGRB 2002, Geyer & Gwinner 2008; see also Table 2.1). Soils are shallow, both on the slopes and on the plateau (Table 2.2). The main soil type is rendzina.

During the 18th and beginning of the 19th century there was a great increase in area of arable land due to the increasing human population after the strong decrease in the 17th century (the Thirty Years' War, pest epidemies). Cultivation of marginal areas, however, was very labour-intensive. In the case of "Kaltes Feld", the fields the farmers were cultivating were located some 200 to 300 altitudinal meters higher than their farms. Therefore, arable farming of distant and less fertile fields was abandoned in the middle of the 19th century when the first railways were constructed connecting rural areas with central market places and farm products were imported from more fertile regions (Mailänder 2005). At the same time, the "golden age" of sheep breeding inWuerttemberg started, which means that arable fields were turned rapidly into grasslands. Later in the 19th century, mineral fertilizers were introduced, which caused further abandonment of marginal areas (Poschlod et al. 2010). The last massive abandonment of arable fields in the study area occurred afterWorldWar II when the economic situation improved (Poschlod&Wallis de Vries 2002, Mailänder 2005).

Crops which were mostly cultivated in the past in the study region were spelt (*Triticum spelta*) and oat (*Avena sativa*), potatoes (*Solanum tuberosum*), clover (*Trifolium pratense* but also *Medicago sativa*) and sainfoin (*Onobrychis viciifolia*) (Königliches statistisch-topographisches Bureau 1870, Gradmann 1950). The grasslands belong to the broadly conceived association *Gentiano-Koelerietum* (alliance *Mesobromion erecti*), which is a typical example of mesophilous Central European calcareous grasslands (Oberdorfer 2001, Chytrý et al. 2007). Flora and vegetation of the study area were already described by Alexejew et al. (1988) and Jandl (1988).

Study sites

Ancient and recent grasslands were selected using cadaster maps from 1830, and land-use maps from 1953 and 2002 which were made available by Mailänder (2005). As ancient grasslands patches we considered grasslands which were continuously marked as pastures since 1830. Recent grasslands were defined as patches which were marked as arable land at least on one of the older maps (1830, 1952) and as grasslands at least on the most recent map (2002).

Ten ancient and 12 recent grasslands were selected. The higher number of recent grasslands was chosen due to generally greater variability of them (e.g., inclination, age, see also Table 2.2 and Fig. 2.2). Four recent grasslands on the plateau were exactly 150 years old (category "very old" grassland), four other grasslands were between 55 and 150 years ("old" grassland) and four grasslands only about 50 to 60 years old ("young" grassland). The ancient and recent grasslands selected were roughly similar in terms of environmental characteristics like slope, exposure and soil depth.

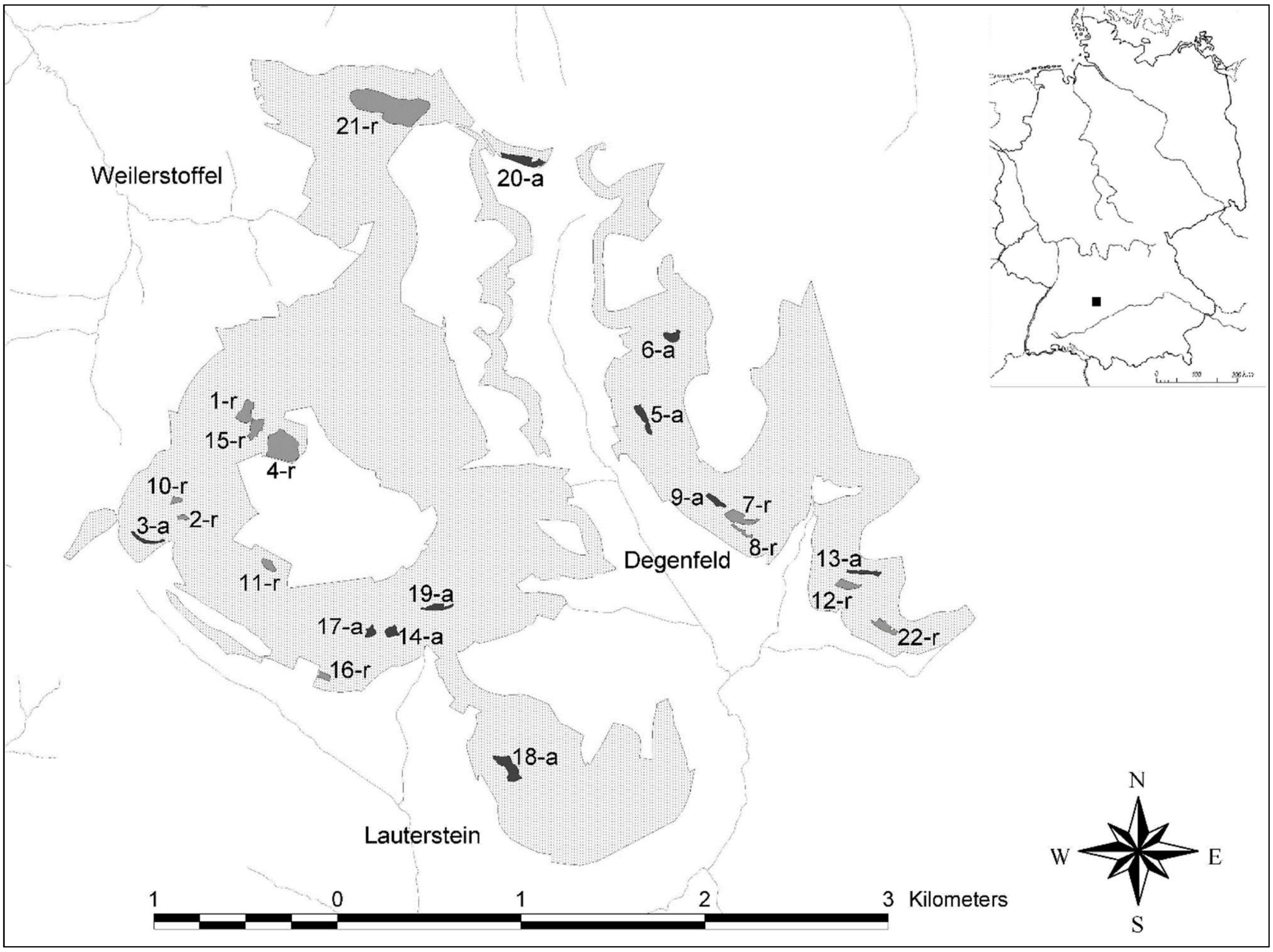

Fig. 2.1. – Location of "Kaltes Feld" in Germany and that of the investigated ancient (dark grey, a) and recent (grey, r) grasslands in the study area. Bright grey area is the nature conservation area. Position of brooks and villages are also shown.

Table 2.1. – Geology of the localities.

Geology	Number of ancient grasslands plots	Number of recent grasslands plots
kimmeridgian marl-stone (ki1)	32	20
oxfordian marl stone (ox1)	10	5
solid limestone (ox2)	1	15
hard reef-limestone (joMu)	0	20
run-of-hill scree (qu)	7	0

Table 2.2. – Data of environmental variables in different age classes of grasslands. One-way ANOVA was applied to test for significant differences between at least two groups followed by Tukey HSD multiple comparisons. Different letters indicate significant differences between age classes. SD: Standard deviation; P: significance value; *** p<0.001; ** p<0.01; *p<0.05. ; ns.: result not significant. EIV = Ellenberg indicator value.

Variable	Ancient grasslands (N=50)		Very old (1855, plateau) (N=20)		Old (<<1953) (N=20)		Young (>1937,>1953) (N=20)		One-way ANOVA		
		SD	Mean	SD	Mean	SD	Mean	SD	F	p	Sign.
Mean Species number	37.52	6.50	40.60 a	4.26	38.05 a	8.62	38.80 a	6.07	1.10	0.352	ns.
Shannon-Wiener Index	3.15 a	0.22	3.18 a	0.20	3.03 a	0.38	3.10 a	0.25	1.44	0.234	ns.
Altitude (m a.s.l.)	665 ac	15.3	773 b	6.17	666 ac	30.23	650 c	36.92	131.33	<0.001	***
Exposition (°)	210 a	31.9	222 a	100.02	229 a	69.61	189 a	14.59	1.98	0.122	ns.
Inclination (°)	17.82	5.70	2.80 b	2.17	14.80 ac	8.34	12.15 c	4.96	33.53	<0.001	***
Soil depth (average; cm)	18.55	7.30	13.63 b	3.25	18.81 a	5.85	13.06 b	3.81	6.73	<0.001	***
Cover herb layer (%)	77.18	10.1	77.35 a	11.09	84.35 a	13.42	80.90 a	11.22	2.31	0.081	ns.
Cover moss layer (%)	9.20 a	6.23	15.10 ab	10.95	12.40 a	12.85	7.30 ac	5.32	3.53	0.017	*
Cover of stones (%)	2.66 a	5.20	0.00 bc	0.00	0.85 ac	2.01	0.00 bc	0.00	4.12	0.008	**
PDSI 21. December	3,30 a	0,88	1.72 b	0.19	2.74 a	1.30	3.01 a	0.57	16.57	<0.001	***
PDSI 21. March	6.26	0.58	5.13 b	0.17	5.83 cd	0.93	6.08 acd	0.41	18.29	<0.001	***
WHC (weight %)	59.92	9.08	81.61 b	9.29	67.23 a	10.05	73.14 b	15.95	21.29	<0.001	***
pH(H_2O)	7.60 a	0.08	6.84 b	0.58	7.57 ac	0.10	7.40 c	0.25	39.31	<0.001	***
pH($CaCl_2$)	7.28 a	0.06	6.58 b	0.61	7.27 a	0.10	7.11 a	0.26	30.63	<0.001	***
H_2O-$CaCl_2$	0.32 a	0.09	0.26 a	0.13	0.29 a	0.10	0.29 a	0.09	2.17	0.096	ns.
Conductivity (µS)	130 a	15.8	86 b	31.22	117 a	14.66	133 a	25.35	23.78	<0.001	***
K (mg/kg soil)	158 a	45.6	54 b	28.96	160 a	49.44	143 a	51.05	27.90	<0.001	***
P (mg/kg soil)	18.51	6.35	8.23 b	3.49	19.03 a	6.45	17.43 a	6.72	15.69	<0.001	***
EIV Light	7.40 a	0.08	7.32 b	0.08	7.31 b	0.05	7.32 b	0.12	9.71	<0.001	***
EIV Temperature	5.48 a	0.08	5.44 a	0.10	5.54 b	0.11	5.65 c	0.05	23.37	<0.001	***
EIV Continentality	3.72 a	0.10	3.60 b	0.15	3.86 c	0.13	3.87 c	0.15	21.24	<0.001	***
EIV Moisture	3.89 a	0.14	4.09 b	0.15	3.87 a	0.21	3.87 a	0.11	10.77	<0.001	***
EIV Soil reaction	7.48 a	0.09	6.91 b	0.25	7.45 a	0.13	7.43 a	0.17	71.70	<0.001	***
EIV Nutrients	2.91 a	0.18	3.52 b	0.29	3.04 a	0.17	3.36 b	0.20	53.37	<0.001	***

Vegetation data

Vegetation was recorded during July-August in seasons 2006 and 2007 on five 2m x 2m plots placed semi-randomly (with exclusion of rock, bush or strongly disturbed patches) in each grassland applying the Braun-Blanquet's (1964) 9 grade abundance-dominance scale. For the data processing scale classes were transformed into percent values: 1 (r), 2 (+), 3 (1), 5 (2a), 8 (2m), 18 (2b), 38 (3), 63 (4), and 88 (5). For each plot we calculated species diversity using number of species (species richness) and Shannon-Wiener index. The Shannon–Wiener index of diversity (Begon et al. 1990) was calculated in CANO-DRAW (ter Braak & Šmilauer 2002).

Species occurring only in one plot (see Appendix) were excluded from multivariate analysis because they do not contribute to the explanation of vegetation patterns. This concerns 21 species of in 163 taxa in total. Four species (*Rhinanthus minor, R. glacialis, Polygala vulgaris, P. comosa*) were omitted because they could not be identified to the species level in case they did not flower. Also the hybrid *Ononis spinosa* x *repens* was omitted. Therefore, 137 taxa were included in the analysis.

Nomenclature follows Rothmaler (2005) for species and Oberdorfer (2001) for syntaxa.

Environmental data

For each plot data on environmental parameters were collected. This included geological substrate, altitude, inclination, exposition, cover of herb- and moss-layer, cover of stones, occurrence of ant-hills and two categories of current management (grazing or no grazing; shrubs cleared or not cleared). Most localities of both, ancient and recent grasslands were underlain by marl-stone. Some localities occurred on solid limestone and on other rocks (see Table 2.1).

Data on latitude, inclination and exposure were used to calculate the potential direct solar radiation (PDSI). This was done by adding the cosines of angles between the sun and the plot surface at 15-minute intervals over a whole day. The calculation was done on the 21st day of each month between December and June following the description of Jeník & Rejmánek (1969). Most of the variability in species data was explained by winter months (December to March) probably due to the effect of the thickness and duration of the snow cover. Furthermore, the following soil physical and chemical properties were measured for each plot: soil depth, water holding capacity (WHC), pH(H2O), pH(CaCl2), conductivity, concentration of available potassium (K) and phosphorus (P) in the soil.

Soil depth was estimated by repeatedly (8 ×) thrusting an iron rod, 0.6 cm in diameter, into the soil. Water holding capacity was measured by collecting soil cores using a metal borer of a standard volume of 100 cm3 (diameter 56.4 mm, height 40 mm). After collecting each sample, soil within metal borer was saturated with water by placing on a permanently wet filter paper for 24 hours. Then, the saturated samples were dried at 105°C until a constant weight. Water holding capacity was calculated using the following formula: WHC = (weight of water saturated soil – weight of dry soil) × 100/ weight of dry soil.

For the measurement of soil chemical properties soil from 5 to 10 cm depth was collected at three points within each plot and mixed afterwards. Soil was air dried and sieved through a 2 mm sieve before the analysis. The methods for soil chemical analysis followed the standards given by Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten (1991). Soil reaction (pH) was measured in a 1:2.5 suspension of dry soil and distilled water (active soil acidity) or 0.01 M $CaCl_2$ (exchangeable soil acidity) after 1 hour using universal pH meter WTW SenTix41. Conductivity was analysed in a 1:5 suspension of dry soil and distilled water with a WTW LF340 apparatus. Plant-available P and K were extracted by calcium acetate lactate (CAL). Phosphorus was measured photometrically after making the P content visible with ammoniumheptamolybdate. K was analysed with an atomic absorption spectrometer. Other variables were geographical coordinates and their combinations. This analysis was done to filter out possible spatial distribution effects of samples (Fortin & Dale 2009).

Data analysis

Differences between environmental parameters in grassland-age classes were analysed applying one-way analysis of variance (ANOVA) followed by a Tukey HSD test in SPSS 12.0 Program (Bühl & Zöfel 2000). Unweighted mean Ellenberg indicator values (Ellenberg et al. 1992) for particular plots were calculated using the JUICE 6.5 Program (Tichý 2002) to test for additional variables. Juveniles of trees and shrubs were omitted from this calculation.

Ordination techniques were applied to determine the difference between the vegetation of ancient and recent grasslands and the influence of environmental factors. Methods based on the linear species response were chosen, which was supported by the length of gradient in DCA analysis (less than 3 S.D. units; ter Braak & Šmilauer 2002). Thus, Principal Components Analysis (PCA) and its constrained counterpart, Redundancy Analysis (RDA) were applied using the CANOCO for Windows 4.5 program package (ter Braak & Šmilauer 2002).

To estimate the influence of environmental factors, the eigenvalues of the corresponding ordination axes from unconstrained (PCA) and constrained (RDA) analyses were compared (Lepš & Šmilauer 2003). Scaling is focused on inter-species correlations in order to facilitate visibility of species positions in biplots. Species scores were divided by standard deviation. Species coverages (in percent) were transformed using the formula $y = (\ln x + 1)$. Neither centering nor standardization were used for samples (vegetation plots). Centering, but not standardization was used for species. Statistical significance of first canonical axe in RDA's was determined using the Monte Carlo permutation test, with 1999 permutations and reduced model. Permutations were restricted to the split-plot design. Five vegetation plots within each grassland were not permuted split plots. Particular grasslands represent whole plots and were permuted completely at random. Floristic differences between ancient and young grasslands were analysed using RDA (length of gradient in DCA: 2.292). We used only one explanatory variable, which was „History". Other variables were used as covariables in the RDA in order to filter out different environmental variables and spatial gradients and to obtain only the effect of history on species composition. Significance of all potential covariables was at first tested by manual forward selection with the p-value = 0.05 (Monte Carlo test, 499 permutations). The following environmental variables were selected applying the forward-selection function: Altitude, inclination, soil depth (average), grazing, three variables for geology (joMu, ox2, ki1), PDSI on 21 December, PDSI on 21 February, phosphorus, pH(H_2O), conductivity, cover of herb layer and geographical coordinates X and Y.

All variables except geology and management (grazing) were quantitative data. Geology and management data were categorical. Due to strong correlation with other variables (high Inflationindex in Canoco) altitude and PDSI of 21 February were excluded from the further analysis. Therefore, in total 13 covariables were used for direct gradient analysis (RDA).

Various methods such as regression coefficients, scores on the first canonical axis in $RDA_{history}$ and others were applied to detect indicator species for both, ancient and recent grasslands. These methods offered similar results, therefore, only the results from the fidelity calculation expressed with Phi-coefficient (Sokal & Rohlf 2001, Chytrý et al. 2002) are presented in this paper (Table 2.4). Significance of fidelity for species belonging to ancient or recent grassland was calculated using Fischer`s exact test (p = 0.05). Data were processed using the JUICE 6.5 Program (Tichý 2002).

Results

Vegetation patterns

There were strong differences in ancient and recent grasslands, both in vegetation and environmental variables. The assesment of the basic vegetation pattern was performed by PCA analysis which shows distinct differences between plots of ancient and recent grasslands (ordination diagram not shown). The majority of plots was well separated. The main floristic variability (gradient along first axis AX1) can be interpreted by the variables geology and history (see also Fig. 2.2, 2.3, 2.4). The vegetation pattern can be differentiated into three groups (PCA diagram not shown, see Appendix 2.1). Nearly all plots of the ancient grasslands and only few of recent grasslands are characterised by many basi- and calciphilous grassland species such as *Carex flacca*, *Buphthalmum salicifolium*, *Carlina acaulis* subsp. *caulescens*, *Hippocrepis comosa* and *Ligustrum vulgare.* The plots which include species of this group are characterised by the occurrence on marl-stone (ki1-Lacunosamergel). There are two groups of recent grasslands. The first group is characterised by many mesophilous grassland species such as *Avenula pubescens*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Trisetum flavescens*, *Cerastium holosteoides*, *Trifolium pratense*, *T. repens* and *Veronica chamaedrys,* some acidophilous species such as *Agrostis capillaris* and *Luzula campestris* and few arable weeds and ruderals. This group is related to the 150 years old grasslands on the plateau underlain by slowly weathered reef-stone. Another group of recent grasslands can be identified by its occurrence on mainly solid limestone and by calciphilous species such as *Salvia pratensis, Melampyrum arvense, Centaurea scabiosa* and hemerophilic species as *Medicago sativa* and *Convolvulus arvensis*.

If grasslands were constrained with factor “history” and differentiated into four age classes, the general pattern remained similar (Fig. 2.4). A synoptic table of the original floristic data is provided in the Appendix 2.1.

Environmental variables

Although there were no differences in species diversity parameters, there were clear differences in habitat properties (excepting cover of herb layer and exposition) of ancient and recent grasslands (Table 2.2) which became already obvious from a PCA correlating a larger amount of environmental variables (Fig. 2.2).

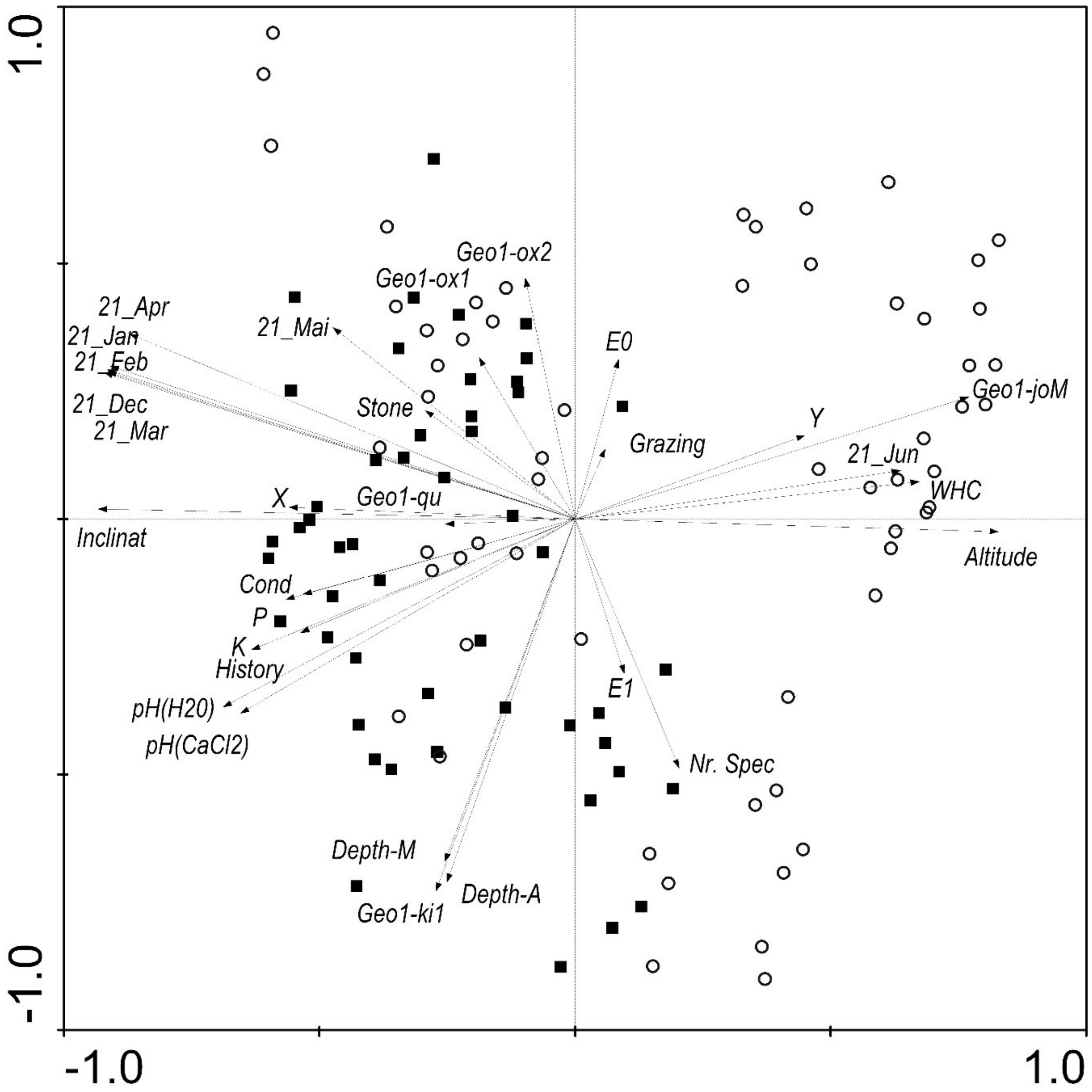

Fig. 2.2. – Principal components analysis (PCA) presenting the correlations between a larger amount of environmental variables (geology [joMu, ox 1, ox2, ki1, qu; see Table 2.1 for details], history, altitude, inclination, PDSI of all seven months, soil depth (average and median), pH(H_2O), pH($CaCl_2$), conductivity, plant available potassium (K) and phosphorus (P), number of species, cover of herb (E1) and moss (E0) layer, cover of stones, grazing and geographical coordinates X and Y in an ordination diagram (squares – ancient grasslands, circles – recent grasslands). Environmental variables were treated like "species".

Ancient grasslands exhibited a higher inclination than recent grasslands. Accordingly, solar radiation was also higher in ancient grasslands. Soil was a little bit deeper in ancient than in recent grasslands. Soils of recent grasslands were more acidic. More information is presented in Table 2.2.

Both, standard deviations of most environmental parameters (Table 2.2) as well as multivariate analysis (Fig. 2.2) show clearly that the environment in recent grasslands is much more heterogenous than in ancient grasslands. If recent grasslands were divided in three age classes, a more differentiated pattern appeared showing that the oldest recent grasslands were situated on the plateau with partly strong differences in several environmental parameters whereas the grasslands from the younger recent grasslands (60 to 150 and 50 to 60 years old) were more similar to ancient grasslands (Table 2.2).

History

The influence of the land-use history was calculated using the direct linear analysis (RDA). History ($RDA_{history}$) explains 2/3 of variability along the main floristic gradient comparing to RDA with all variables. However, history is correlated with other environmental variables when the results of AX1 in both RDA's, $RDA_{history}$ and $RDA_{history+covariables}$, are compared. Therefore, the eigenvalues of the first ordination axes (AX1) from PCA and $RDA_{history+covariables}$ were compared, which showed that 21% of the vegetation pattern along the main floristic gradient could be attributed to the net influence of history. The permutation test of the first axis was highly significant (Table 2.3).

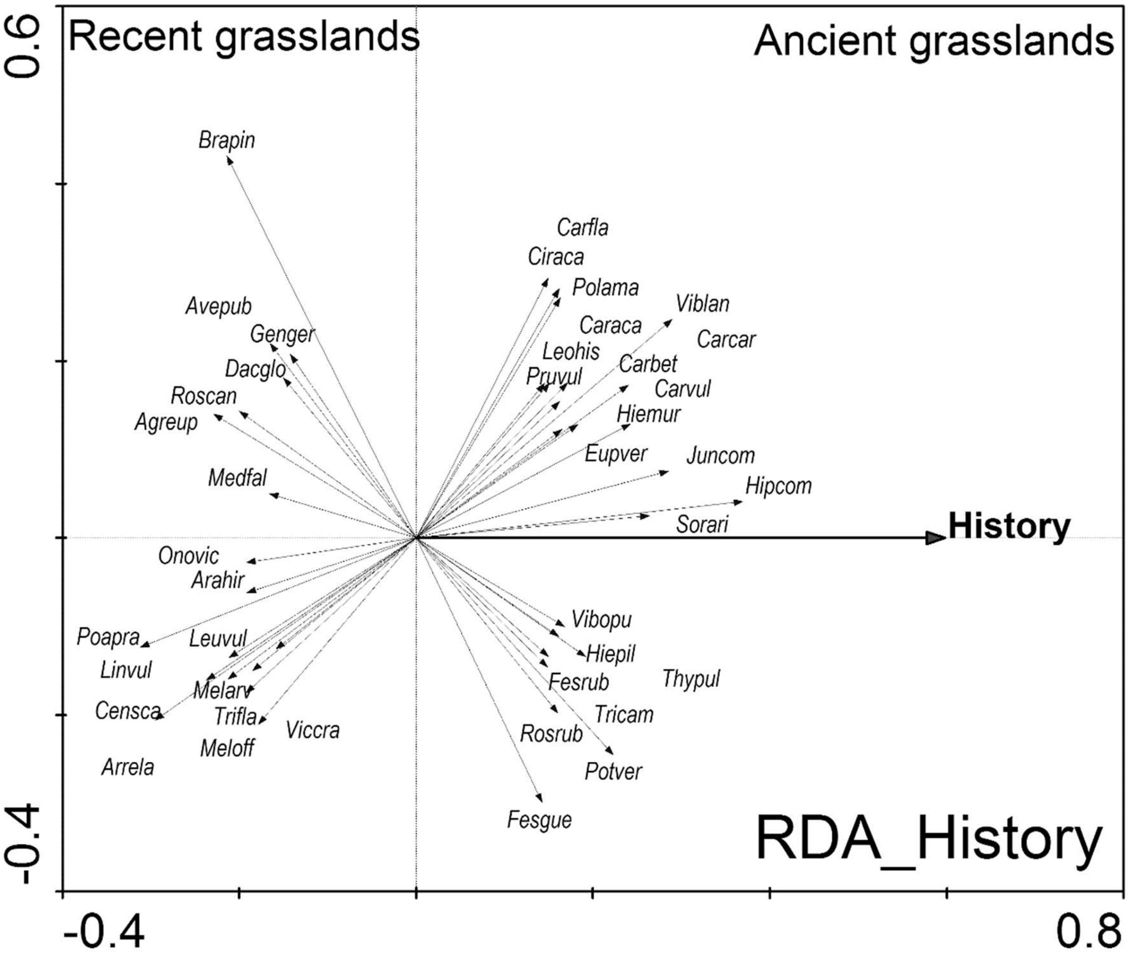

Fig. 2.3. – $RDA_{history+covariables}$ analysis constrained with factor "history", reflecting the continuous ancient grasslands and discontinuous recent grasslands. The effect of 13 covariables was subtracted. Only the 44 most correlated species (species fit range > 10%) are presented. For the full species names see Appendix 2.1.

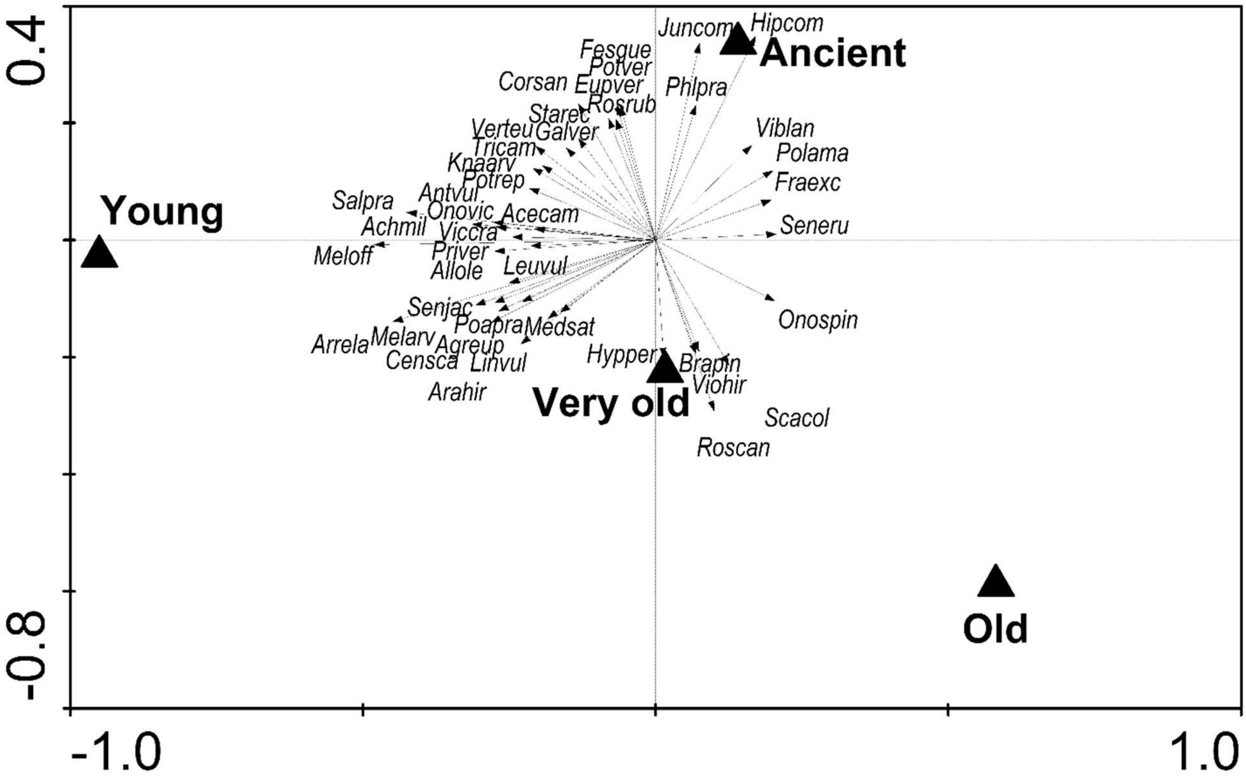

Fig. 2.4. – RDA$_{\text{age groups+covariables}}$ analysis constrained with four variables representing different age-groups of grasslands. “Ancient” grassland are continuously used as pastures at least since 1830. Category “very old” represent exactly 150 years old grasslands, “old” represent grasslands between 55 and 150 years and “young” means grasslands only about 50 to 60 years old. The effect of covariables was subtracted. Only the 43 most correlated species (species fit range > 4%) are presented. For full species names see Electronic Appendix 1.

Table 2.3. – Results of the ordination analysis (PCA, RDA). Plots n = 110, species n = 137, environmental variables and covariables n = 14 (history, three variables for geology, inclination, PDSI on 21 December, average soil depth, pH(H2O), conductivity, phosphorus, cover of herb layer, grazing and geographical coordinates X and Y). For detailed explanation see text and Figs 2–4; %variance: cumulative percentage variance of species data explained by four ordination axes, % all AX: variance explained by all the canonical axes, F-statistics and significance (p-value) of Monte Carlo permutation test of significance of first canonical axis (1.999 permutations under reduced model).

Ordination analysis	Environmental variables	Covari-ables	% variance				% all AX	F-stat	p-value
			AX1	AX2	AX3	AX4			
PCA	-	-	16.3	26.2	33.3	38.6	-	-	-
RDA	14	0	13.7	22.2	26.6	30.5	42.7	15.118	<0.001
RDA$_{\text{history}}$	1	0	9.4	20.1	29.6	35.7	9.4	11.162	<0.001
RDA$_{\text{history+covariables}}$	1	13	3.5	10.4	16.5	21.5	3.5	3.481	<0.001
RDA$_{\text{age groups}}$	4(3)	0	12.7	18.8	21.1	30.5	21.1	15.490	<0.001
RDA$_{\text{age groups+covariables}}$	4(3)	13	3.9	6.9	8.7	14.8	8.7	3.763	<0.001

Indicators for ancient and recent grasslands

On the RDA$_{\text{history+covariables}}$ biplot (Fig. 2.3) species are shown according to their position along the first canonical axis constrained by history. On the left side of the diagram species typical for recent grasslands are displayed, in contrast to this group on the right side species typical for ancient grasslands. The application of different analyses to calculate the indicator value of species related to history such as fidelity expressed by Phi coefficient, regression coefficients or scores on the first canonical axis in $RDA_{history}$ provided similar results. Therefore, only the results from the fidelity analysis are presented here (Table 2.4). This analysis clearly show that in the case of ancient grasslands indicators were nearly not exclusive which was, however, the case in recent grasslands.

Strong indicators for ancient grasslands were *Carex caryophyllea*, *C. flacca, Bupthalmum salicifolium, Carlina vulgaris, Cirsium acaule, Hippocrepis comosa* and *Scabiosa columbaria*. Species exclusively indicating recent grasslands are *Anthoxanthum odoratum, Avenula pubescens*, *Cynosurus cristatus*, *Dactylis glomerata*, *Cerastium holosteoides*, *Medicago sativa*, *Melampyrum arvense*, *Onobrychis viciifolia*, *Rhinanthus alectorolophus* and others. The RDA indicated a different indicator strength for some species when environmental covariables were subtracted due to the preference/non-preference of species for specific environmental conditions. Such substraction allows a better detection of the real effect of history. When covariables are substracted the following species of both ancient and recent grasslands had a remarkably lower indicating power: *Achillea millefolium*, *Agrostis capillaris, Cynosurus cristatus*, *Galium molugo* and *Trifolium pratense* (all from recent grasslands occurring on the plateau), *Daucus carota* and *Scabiosa columbaria* (both from ancient grasslands growing on soils with higher pH and relatively high content of nutrients, especially potassium). However, other species had a stronger indicating power after substraction of covariables. These were species growing under intermediate environmental conditions such as e.g., *Thymus pulegioides* s.str. and *Viburnum lantana* in ancient grasslands or *Centaurea scabiosa, Medicago sativa*, *Melampyrum pratense* and *Onobrychis viciifolia* in recent grasslands.

Table 2.4. – Synoptic table including indicator species of both ancient and recent grasslands. Species are sorted by a fidelity measure (presence/absence data) expressed in terms of the Phi coeficient (calculation by JUICE 6.5 Program; Tichý 2002). Only those species with significant fidelity to each group are listed (P = 0.05; Fischer's exact test). Number of plots n = 50 for ancient and 60 for recent grasslands. The percentage frequency of each species in each group is given.

Indicators of ancient grasslands				
	fidelity ancient	fidelity recent	frequency, ancient	frequency, recent
No. of relevés:	50	60	50	60
Species				
Hippocrepis comosa	76.2	---	94	18.3
Buphthalmum salicifolium	50.7	---	74	23.3
Carlina vulgaris	48.4	---	60	13.3
Carex flacca	44.7	---	100	66.7
Prunella vulgaris	43.1	---	82	40
Juniperus communis	42.9	---	44	6.7
Carex caryophyllea	38.2	---	98	70
Hieracium pilosella	37.4	---	50	15
Cirsium acaule	36.1	---	96	68.3
Scabiosa columbaria	34.6	---	90	60
Daucus carota	31.7	---	76	45
Briza media	31.2	---	94	70
Viburnum lantana	29.5	---	16	.
Senecio erucifolius	28	---	40	15
Carlina acaulis subsp. *caulescens*	27	---	62	35
Linum catharticum	27	---	98	81.7
Leontodon hispidus	26.7	---	84	60
Gymnadenia conopsea	26.1	---	38	15
Polygala amarella	25.5	---	28	8.3
Koeleria pyramidata	23.9	---	48	25
Ligustrum vulgare	23.9	---	48	25
Potentilla neumanniana	23.7	---	76	53.3
Euphorbia verrucosa	23	---	14	1.7
Rosa rubiginosa	22.9	---	10	.
Thymus pulegioides subsp. *pulegioides*	20.9	---	100	91.7
Aster amellus	20.5	---	12	1.7
Sorbus aria agg. – juv.	20.5	---	12	1.7
Gentiana verna	20.4	---	8	.
Brachypodium pinnatum	19.2	---	92	78.3
Vincetoxicum hirundinaria	18.3	---	60	41.7

Indicators of recent grasslands				
	fidelity ancient	fidelity recent	frequency, ancient	frequency, recent
No. of relevés:	50	60	50	60
Species				
Trisetum flavescens	---	65.6	4	66.7
Veronica chamaerdys	---	56	2	51.7
Poa pratensis subsp. *angustifolia*	---	44	26	70
Dactylis glomerata	---	43.8	16	58.3
Festuca pratensis	---	43.5	4	40
Cerastium holosteoides	---	40.6	.	28.3
Avenula pubescens	---	39.2	.	26.7
Cynosurus cristatus	---	39.2	.	26.7
Vicia cracca	---	38.2	2	30
Anthoxanthum odoratum	---	37.8	.	25
Salvia pratensis	---	37.8	.	25
Agrostis capillaris	---	36.3	.	23.3
Arrhenatherum elatius	---	36.3	.	23.3
Cirsium eriophorum	---	34.9	.	21.7
Trifolium pratense	---	33.4	44	76.7
Luzula campestris	---	33.3	.	20
Ononis repens	---	32.1	2	23.3
Senecio jacobea	---	32.1	2	23.3
Agrimonia eupatoria	---	31.4	48	78.3
Trifolium repens	---	30.4	2	21.7
Rhinanthus alectorolophus	---	30.2	.	16.7
Hypericum perforatum	---	29.1	18	45
Galium verum	---	28	8	30
Convolvulus arvensis	---	26.7	.	13.3
Thymus pulegioides subsp. *carniolicus*	---	26.7	.	13.3
Galium mollugo s.l.	---	26.1	14	36.7
Euphrasia sp.	---	25.2	2	16.7
Galium pumillum	---	25.1	20	43.3
Cerastium arvense	---	24.9	.	11.7
Potentilla reptans	---	24.9	.	11.7
Medicago lupulina	---	24	50	73.3
Acer campestre – juv.	---	23.3	10	28.3
Arabis hirsuta	---	23.3	2	15
Arenaria serpyllifolia	---	22.9	.	10
Centaurea scabiosa	---	22.9	.	10
Melampyrum arvense	---	22.9	.	10
Melilotus officinalis	---	22.7	6	21.7
Taraxacum sect. *Ruderalia*	---	21.5	10	26.7
Medicago sativa	---	20.9	.	8.3
Onobrychis vicifolia	---	20.9	.	8.3
Trifolium campestre	---	20.9	.	8.3

Discussion

Vegetation pattern, history and environmental parameters

There were no differences in species richness in ancient and recent grasslands, however, species composition strongly differed. These differences could be assigned to both habitat properties and history. Percentages of explained variability on AX1 by particular variables in the RDA analysis without covariables were: Geology (marlstone x other) 10.9; Geology (hard reef-limestone x other) 10.7; Altitude 9.5; History (ancient x recent) 9.4; pH(H_2O) 9.1; Inclination 8.5; PDSI 21.March 7.0 (see also Fig. 2.2 for correlations between variables).

The relationship between the vegetation of grasslands and former land use was still very clear and significant if the influence of other variables was subtracted (Table 2.3). The influence of history was even stronger, 4.8 instead of 3.5%, when the four recent grasslands situated on the plateau, which is strongly affected by other environmental parameters such as geology, were omitted. A similar strong effect of history on the composition of the vegetation is reported byHermy et al. (1999),who compared ancient and recent forests.

The geomorphological and soil parameters of the ancient and recent grasslands also differed. Arable field use was correlated often with a lower inclination – although some recent grasslands occurred on steep (> 20°) slopes – which are not only easier to plough but also are less affected by soil erosion. Despite this soil depth is significantly lower in recent grasslands, which clearly shows that soil erosion occured during the arable field phase. There was a slight positive correlation between soil depth and slope inclination (Pearson correlation coefficient $r = 0.229$, $P = 0.016$, $n = 110$). Based on many local studies, Bork et al. (1998) reveal that soil erosion occurred in historical times to a much greater extent than today and argue that this is because (i) the area of arable fields was much greater and (ii) the plant cover of arable fields was less dense.

Whereas there were no differences in the cover of the herb and moss layers, cover of stones was significantly different, reflecting the fact that during the period of arable field use stones were removed by hand, often still visible at the edges of recent grasslands or in recent forests, where there are deposits of long heaps of stones.

In terms of soil physical and chemical properties those of recent grasslands have a higher water holding capacity than those of ancient grasslands. This fact can be explained by the geological substrate of most of the ancient grasslands, which is marlstone, and the resultant soil dense and loamy. Higher water holding capacity may explain the higher number of mesic grassland species. Contents of potassium and phosphorus, the latter often the limiting factor on calcareous soils (Janssens et al. 1998, Carroll et al. 2003), were significantly lower in the very old grasslands due to the specific abiotic conditions prevailing on the plateau (Table 2.2). However, other authors report high nutrient levels in soil even after almost 2000 years of arable field use (Dupouey et al. 2002). In our case nearly no fertilizer was applied, because of the great altitudinal difference between farms and fields, except that provided by occasional hurdling by sheep during the stubble phase, which was still the case even during the 1950s (Mailänder 2005). Finally, tillage caused the decomposition of humus and harvesting of crops continuously extracted nutrients. This pattern, however, contrasts with the vegetation pattern of recent grasslands, where there are more species indicating rather high nutrient supply (N-value, Table 2.2). These indicators are particularly associated with the plateau (“very old” grasslands). This might be explained by the fact that highly productive species are also able to thrive at low phosphorus concentrations (from 20 mg P/kg soil; Hejcman et al. 2007, 2009) and that the indicator values for terrestrial plants only take into account nitrogen and ignore the fact that P and K may be limiting under certain conditions (Schaffers & Sýkora 2000, Niinemets & Kull 2005, Chytrý et al. 2009).

Vegetation patterns and flora

Differences in vegetation patterns were associated with ecological or phytosociological plant species groups. Recent grasslands were phytosociologically more heterogenous and, unlike ancient grasslands, could not clearly be assigned to a certain community. Ancient grassland species could be clearly assigned to *Festuco-Brometea* (Oberdorfer 2001, Chytrý & Tichý 2003), whereas recent grassland species belong to different classes, namely *Festuco-Brometea* but also *Molinio-Arrhenatheretea, Trifolio-Geranietea sanguinei* and *Secalietea cerealis* or even crop plants.

The occurrence of arable weed species in recent grasslands, such as *Convolvulus arvensis*, *Cerastium arvense* and the hemiparasitic species, *Melampyrum arvense* and *Rhinanthus alectorolophus*, strongly feared in former times since they strongly decreased crop yield (Gradmann 1950), is reported by other authors (Dutoit & Alard 1995, Poschlod & Wallis de Vries 2002, Dutoit et al. 2004). However, formerly cultivated plants like *Dactylis glomerata*, *Medicago sativa*, *Melilotus officinalis*, *Onobrychis viciifolia* and/or *Trifolium pratense*, still occur in recent grasslands; the last one, however, is also frequent in ancient grasslands (Table 2.4, Electronic Appendix 2.1). Some of these species are not indigenous. *Melilotus officinalis* is an archaeophyte and was probably introduced with unclean seed (Lohmeyer & Sukopp 1992). *Onobrychis viciifolia* is a neophyte and was introduced as a fodder plant (Kowarik 2003). Cultivation of *Dactylis glomerata* started in the 18th century (Stebler & Schröter 1902). *Medicago sativa* and *Trifolium pratense* were widely grown as fodder plants on nutrient-poor soils and are even mentioned as cultivated in the study region (Königliches statistisch-topographisches Bureau 1870, Gradmann 1950). *Melilotus officinalis* was often sown because of its medicinal properties, as a bee plant and to improve soil conditions. The medical power of field melilot was well known even in prehistorical times. In certain regions it was delivered in huge quantities to pharmacies and drugstores (Hegi 1966). The cultivation of *Onobrychis viciifolia* started in France during the 15th century and in Germany at the beginning of the 18th century, especially on nutrient-poor calcareous soils, which made it possible for the first time to transform calcareous grassland intomore productive arable fields for fodder production (Stebler& Schröter 1902).

The largest proportion of recent grassland species are either mesotrophic (*Molinio-Arrhentheretea*) or calcareous (*Festuco-Brometea*) grassland species like *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Avenochloa pubescens*, *Cerastium holosteoides*, *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Poa pratensis*, *Trisetum flavescens*, *Trifolium pratense*, *Vicia cracca* or *Arabis hirsuta*, *Ononis repens*, *Salvia pratensis*, *Thymus pulegioides* subsp. *carniolicus*. *Salvia pratensis* and *Centaurea scabiosa*, both diagnostic species of *Festuco-Brometea*, occurred only in the most recent grasslands, which are 50–60 years old. The absence in ancient grassland can be explained by the fact that these species rarely naturally occur at higher altitudes such as in the study area. Their occurrence in recent grasslands may be explained by tradition of hayseed application after abandonment of arable field use, which was applied extensively during the 19th and beginning of the 20th century, the period of the famous grassland construction schools in Germany (Häfener 1847, Hard 1964, Schröder-Lembke 1983, Poschlod&Wallis de Vries 2002). In contrast to recent grasslands, characteristic species of ancient grasslands were mainly typical calcareous grassland species (Table 2.4). These indicator species patterns correspond to those reported by Röder et al. (2006) based on a comparison of one ancient and one recent grassland located at Garchinger Haide north of Munich.

As there are species of plants that are exclusive indicators of ancient forests (Wulf & Kelm 1994) it is surprising that there are no such indicators for old grasslands. However, this may be due to the fact that recent grasslands were not strongly isolated from ancient grasslands and sheep grazing in the study area maintained a continuous seed input from ancient to recent grasslands. Sheep are known to be one of the most important and effective dispersal vectors in Central-European man-made landscapes (Fischer et al. 1996, Poschlod et al. 1996, Poschlod&Bonn 1998). There are, however, many exclusive species of recent grasslands, which may be simply explained by their former conversion into arable fields, which resulted in the establishment of new species and once established they have persisted even though the habitat has changed.

Conclusions and perspectives

Summarizing, history affects the vegetation pattern more than environment, except for the recent grasslands on the plateau. Therefore, future vegetation studies should include the results of not only floristic and environmental but also historical analyses. Contrary to the commonly held opinion that more recent habitats have little or no nature conservation value (Waesch & Becker 2009), recent grasslands may contain rare and/or endangered species such as *Gentianella germanica*, *Gymnadenia conopsea* and in the case of *Melampyrum arvense* even an exclusive species. Furthermore, a part of the regional calcareous grassland species pool was also restricted to recent grasslands (e.g., *Thymus pulegioides* subsp. *carniolicus*, *Rhinanthus alectorolophus*, *Stachys alpina*). Therefore, recent grasslands may have a high conservation value and should be considered in future management plans of calcareous grassland landscapes.

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Appendix 2.1. – Synoptic table with percentage constancy and median cover of each grassland site calculated from data of five plots/grassland. Median cover r, +, 1, a = 2a, b = 2b, 3.

Grassland No.		6	5	9	20	3	18	14	13	19	17	4	15	1	11	24	10	2	12	7	8	21	16
Age		**Ancient**										**Very old (1855, plateau)**				**Old (>>1953)**				**Young (<1937, <1953)**			
Species	Abbrev.																						
Alliance *Bromion erecti*																							
Bromus erectus	Broere	100 b	100 b	100 b	100 b	100 a	100 b	100 b	100 b	100 b	100 3	100 3	100 b	100 b	100 1	100 b	100 a	100 b	100 3	100 b	100 b	100 3	100 3
Brachypodium pinnatum	Brapin	80 1	80 a	100 +	100 a	100 1	100 +	100 +	100 a	60 +	100 +	.	80 1	80 1	100 1	100 a	100 3	100 a	80 +	100 a	100 1	.	100 +
Sanguisorba minor	Sanmin	40 +	60 +	80 +	100 +	100 +	100 1	100 +	100 +	100 +	100 +	80 +	60 +	80 +	40 +	100 +	80 +	60 +	100 +	100 +	100 +	100 +	100 +
Linum catharticum	Lincat	100 1	100 +	100 1	100 +	100 +	100 +	100 1	100 +	100 +	80 +	40 +	100 +	100 1	40 +	100 +	100 +	100 1	40 r	100 1	100 +	60 +	100 +
Cirsium acaule	Ciraca	100 b	80 a	100 a	100 a	100 1	100 a	100 +	100 a	100 a	80 1	80 +	100 1	100 b	80 +	100 1	100 1	100 1	20 +	100 a	20 1	.	20 r
Festuca ovina subsp. *guestfalica*	Fesgue	80 1	60 a	100 a	100 a	40 r	100 a	100 a	100 +	100 b	100 +	80 1	60 +	80 +	60 1	100 1	80 1	100 1	100 1	100 a	100 1	100 a	.
Euphorbia cyparissias	Eupcyp	100 +	100 1	80 +	60 1	100 1	100 +	100 1	100 +	100 1	100 +	100 a	100 1	100 1	100 a	100 1	100 1	100 1	100 +	100 1	100 +	80 +	40 +
Ononis spinosa	Onospi	100 a	100 a	100 a	100 a	100 a	.	.	40 +	20 +	20 +	.	.	40 r	40 a	100 a	100 a	100 1	40 +	100 a	.	40 +	.
Agrimonia eupatoria	Agreup	80 r	40 r	60 r	80 +	.	.	60 r	80 +	40 r	40 r	80 +	100 +	60 +	80 +	40 r	60 r	80 r	80 r	100 a	100 +	100 +	60 +
Viola hirta	Viohir	40 +	60 +	20 +	40 +	80 r	100 +	80 +	100 1	40 +	80 +	40 r	80 1	80 r	80 a	100 +	100 1	80 r	60 r	40 +	80 +	.	100 1
Koeleria pyramidata	Koepyr	60 +	20 +	60 +	100 +	40 +	80 +	40 +	40 r	40 +	.	.	20 +	20 +	40 r	20 1	80 1	100 1	.	20 a	.	.	.
Carlina acaulis subsp. *caulescens*	Caraca	100 +	100 1	60 +	20 +	40 +	80 +	80 1	20 +	80 +	40 +	.	40 +	40 r	80 +	100 1	40 +	80 1	.	40 +	.	.	.
Carlina vulgaris	Carvul	60 r	60 r	100 +	80 1	80 r	80 +	60 r	.	60 +	20 r	.	.	.	.	20 r	.	20 +	.	40 r	40 r	.	40 r
Bupthalmum salicifolium	Bupsal	80 +	100 1	100 a	100 1	80 +	100 a	80 r	100 a	.	.	.	.	.	.	100 3	.	40 +	20 +	100 +	20 +	.	.
Hippocrepis comosa	Hipcom	60 1	80 1	100 1	100 1	100 a	100 1	100 a	100 1	100 1	100 1	.	.	.	.	40 r	20 1	80 +	20 +	.	.	.	60 +
Medicago falcata	Medfal	20 1	20 1	.	.	.	40 r	20 r	100 +	60 +	.	.	.	.	.	40 r	.	20 +	100 1	60 +	.	20 r	100 +
Aster amellus	Astame	.	.	.	.	.	20 +	.	100 a	.	.	.	.	.	.	20 r	.	.	.	.	.	.	.
Gentiana cruciata	Gencru	.	.	.	.	40 r	.	40 r	.	20 r	40 +	.	20 +	.	.	.	20 +	20 +	.	.	.	.	20 +
Gentianella germanica	Genger	20 +	.	.	40 r	20 r	.	.	.	.	.	.	.	.	.	.	40 +	20 1	.	.	.	.	.
Inula salicina	Inusal	.	.	.	.	20 +	.	20 +	.	.	20 b	.	.	.	.	.	.	.	.	20 +	.	.	.
Stachys recta	Starec	.	.	.	.	.	.	.	.	.	40 +	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum nummularium s.l.	Helova	.	.	.	.	.	.	.	20 1	20 a	.	.	.	20 +	.	.	.	.	.	.	20 +	.	.
Anthyllis vulneraria	Antvul	.	.	20 r	.	.	.	20 r	.	.	.	.	.	.	.	.	.	.	.	40 r	.	.	40 +
Avenula pratensis	Avepra	20 +	20 +	.	.	.	.	.	.	.	.	20 +	20 a	.	80 a	.	20 +	.	.	20 +	.	.	.
Thymus pulegioides subsp. *carniolicus*	Thycar	.	.	.	.	.	.	.	.	.	.	.	60 +	20 +	20 r	.	40 r	20 1	.	.	.	.	.
Onobrychis vicifolia	Onovic	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	20 +	.	40 +	20 r	.	.
Salvia pratensis	Salpra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	60 +	100 1	80 b	40 +
Centaurea scabiosa	Censca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	100 a
Alliances *Bromion* and *Arrhenatherion*																							
Plantago media	Plamed	80 1	80 +	100 1	100 +	100 +	100 +	80 +	40 r	80 1	20 r	100 +	100 +	100 1	60 +	80 +	100 +	80 +	20 +	80 a	80 +	80 +	100 +
Achillea millefolium	Achmil	.	80 +	60 +	60 +	40 r	100 +	100 +	100 +	100 +	100 r	100 +	100 +	100 a	80 +	100 +	100 +	60 +	.	100 +	100 +	100 a	100 +
Lotus corniculatus	Lotcor	100 1	100 1	100 1	100 1	100 +	100 +	100 +	100 +	100 1	100 +	80 +	100 1	100 +	100 +	100 1	100 1	100 1	80 +	100 +	80 +	100 1	100 1
Pimpinella saxifraga	Pimsax	40 +	80 +	100 +	100 +	60 +	80 +	100 +	100 +	100 +	80 +	60 +	100 1	80 +	100 1	80 +	100 +	100 1	100 +	80 +	80 +	80 +	100 +
Ranunculus bulbosus	Ranbul	60 +	80 1	40 r	.	20 +	60 r	20 +	40 r	80 +	.	80 r	60 +	80 +	.	60 +	60 r	60 +	20 +	80 +	40 r	100 r	.
Centaurea jacea	Cenjac	60 1	100 +	80 +	80 1	100 +	100 +	100 a	100 a	.	20 b	.	.	20 +	.	80 1	100 +	80 a	100 +	100 1	100 +	40 +	80 a
Poa pratensis subsp. *angustifolia*	Poapra	20 +	40 +	.	.	.	40 +	40 +	100 +	.	20 +	80 1	60 +	80 +	60 +	20 +	100 1	80 1	40 +	100 +	80 1	40 1	100 +
Knautia arvensis	Knaarv	.	40 r	.	20 1	80 +	60 +	100 +	80 +	60 +	100 +	60 +	20 1	.	.	20 +	80 +	80 r	20 +	80 +	80 +	100 +	100 +
Alliance *Arrhenatherion elatioris*																							
Daucus carota	Daucar	100 +	40 +	60 +	80 +	80 +	60 +	80 r	80 +	100 +	80 +	.	20 r	.	.	100 +	80 r	80 +	40 r	80 +	60 +	.	80 r
Leucanthemum vulgare s.l.	Leuvul	80 1	100 1	80 1	100 +	.	20 +	40 r	40 1	80 1	20 1	.	20 r	20 a	.	40 1	60 +	100 +	20 +	100 1	80 +	.	100 1
Leontodon hispidus	Leohis	100 1	100 1	60 1	100 1	100 +	100 1	80 +	40 1	100 1	60 +	60 +	100 1	80 1	80 +	80 1	100 +	60 a	.	100 1	40 +	20 1	.
Plantago lanceolata	Plalan	80 1	100 1	80 1	80 +	80 +	100 1	100 a	100 +	100 a	100 1	100 a	100 1	100 a	100 1	100 b	100 +	100 1	40 +	80 +	.	60 1	100 1
Trifolium pratense	Tripra	60 1	100 1	80 1	40 r	.	40 r	40 +	20 +	20 +	40 r	80 +	80 +	100 a	100 +	100 +	80 +	80 +	.	100 a	60 +	100 +	40 r
Dactylis glomerata	Dacglo	20 +	20 +	.	.	.	40 r	40 r	20 +	.	20 1	60 +	80 +	100 +	100 a	.	60 +	60 1	20 +	60 +	20 +	60 a	80 +
Trisetum flavescens	Trifla	.	20 +	20 +	.	.	.	.	.	.	.	100 a	100 1	100 +	100 1	.	100 1	80 +	.	40 +	.	80 +	100 +
Festuca pratensis	Fespra	20 +	20 +	.	.	.	.	.	.	.	.	100 1	80 1	80 1	60 1	.	40 +	60 +	.	20 +	.	20 +	20 +
Veronica chamaerdys	Vercha	.	.	.	.	.	.	.	20 r	.	.	100 a	100 1	100 +	100 +	.	20 +	40 1	.	20 1	40 r	40 r	60 +
Galium mollugo s.l.	Galmol	.	40 +	.	.	.	60 r	.	.	.	40 r	60 +	40 +	40 +	.	.	20 +	20 1	40 r	.	60 r	80 +	80 +
Arrhenatherum elatius	Arrela	.	.	.	.	.	.	.	.	.	.	.	20 +	20 +	.	.	.	.	.	60 +	40 +	40 +	100 +
Festuca rubra agg.	Fesrub	.	40 +	.	.	.	.	.	.	.	.	40 +	.	.	.	.	.	.	.	.	.	.	.
Class *Molinio-Arrhenatheretea*																							
Cerastium holosteoides	Cerhol	.	.	.	.	.	.	.	.	.	.	40 +	100 +	100 +	.	.	.	.	.	20 r	.	60 1	20 +
Cynosurus cristatus	Cyncri	.	.	.	.	.	.	.	.	.	.	80 r	40 +	60 +	80 +	.	.	.	.	.	.	60 +	.
Anthoxanthum odoratum	Antodo	.	.	.	.	.	.	.	.	.	.	100 1	80 +	60 +	60 +	.	.	.	.	.	.	.	.
Avenula pubescens	Avepub	.	.	.	.	.	.	.	.	.	.	60 +	20 +	20 1	80 1	20 r	20 +	60 +	.	20 +	.	20 +	.
Vicia cracca	Viccra	.	.	.	.	.	20 +	.	.	.	.	60 +	.	40 +	.	.	60 +	40 1	.	40 r	100 +	.	20 r
Bellis perennis	Belper	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	60 r	.
Rumex acetosa	Rumace	.	.	.	.	.	.	.	.	.	.	40 +	20 +	.	20 +	.	.	.	.	.	.	.	.
Other species																							
Thymus pulegioides subsp. *pulegioides*	Thypul	100 +	100 a	100 1	100 1	100 +	100 a	100 1	100 1	100 a	100 1	100 +	80 +	80 +	100 +	100 a	100 +	80 +	100 +	100 1	80 +	100 b	80 +
Carex caryophyllea	Carcar	100 a	100 a	100 a	100 a	100 1	100 a	100 a	100 1	100 a	80 +	.	80 a	100 a	100 a	20 +	100 1	100 1	80 +	100 a	80 a	40 +	40 1
Carex flacca	Carfla	100 b	100 1	100 a	100 a	100 b	100 a	100 1	100 a	100 a	100 1	20 r	40 a	100 1	80 1	100 1	100 b	100 a	40 1	100 a	80 1	.	40 +
Briza media	Brimed	100 1	100 1	100 a	100 a	100 +	100 1	80 1	100 +	100 1	60 +	60 +	100 +	100 +	100 +	100 a	100 +	100 +	.	100 1	40 r	40 +	.
Scabiosa columbaria	Scacol	100 1	100 1	20 +	100 +	100 +	80 +	100 +	100 +	100 1	100 +	.	100 +	100 +	60 +	80 1	100 +	80 +	60 r	40 +	20 +	.	80 1
Potentilla neumanniana	Potver	.	20 1	80 +	80 +	80 +	100 +	100 +	100 +	100 1	100 1	60 1	80 +	80 +	40 r	20 +	20 r	20 r	80 +	80 +	40 +	100 1	20 r
Medicago lupulina	Medlup	40 r	60 +	40 +	40 r	.	60 1	40 r	60 +	80 +	80 +	40 r	80 r	80 +	20 r	100 +	80 +	100 +	40 +	40 +	100 +	100 1	100 1
Prunella vulgaris	Pruvul	60 +	100 +	100 +	80 +	60 +	80 +	80 +	100 +	100 +	60 +	.	40 r	20 1	40 +	80 +	80 +	100 +	.	60 +	.	20 +	40 +
Campanula rotundifolia	Camrot	80 +	40 r	60 +	40 +	100 +	100 +	80 +	60 r	.	60 +	40 +	100 +	100 1	80 r	100 +	100 +	80 +	.	60 +	.	.	20 +
Origanum vulgare	Orivul	20 +	80 +	60 1	60 +	40 +	40 +	100 +	80 1	40 +	100 +	.	.	.	.	100 1	40 1	80 1	100 a	80 +	100 1	80 +	100 1
Vincetoxicum hirundinaria	Vinhir	.	.	20 r	40 r	100 +	100 +	100 1	40 +	100 +	100 1	.	.	.	.	80 +	60 r	60 +	100 +	40 r	80 +	.	80 r
Prunus spinosa	Pruspi	.	40 r	20 +	60 +	.	20 r	20 +	40 +	60 +	60 +	.	60 +	20 +	40 +	20 +	.	100 +	80 +	20 1	80 1	.	40 +
Ligustrum vulgare	Ligvul	.	.	.	40 r	100 +	80 1	100 1	40 +	40 +	80 +	.	.	.	.	60 +	20 +	60 r	20 +	.	80 +	.	60 r
Hypericum perforatum	Hypper	.	20 +	20 r	40 r	.	40 +	.	.	20 +	40 r	20 r	20 r	20 r	80 +	60 r	60 +	60 +	80 r	20 r	100 +	20 r	.
Galium pumillum	Galpum	.	20 +	20 +	.	.	60 +	.	100 1	.	.	100 +	100 +	60 1	80 +	100 1	20 +	.	40 r	20 +	.	.	.

Hieracium pilosella	Hiepil	40 +	40 +	20 r	100 a	60 +	60 +	60 +	.	80 +	40 r	60 +	.	60 +	.	.	.	.	.	20 +	.	40 1	.
Senecio erucifolius	Seneru	100 r	60 r	.	40 r	.	.	40 r	60 +	60 +	40 r	.	.	.	.	20 +	40 r	60 +	40 +	.	.	.	20 r
Gymnadenia conopsea	Gymcon	80 r	40 r	.	.	100 +	60 r	40 r	40 r	.	20 r	.	.	.	.	60 r	40 r	40 +	.	.	20 r	.	20 r
Juniperus communis	Juncom	40 +	20 r	60 +	.	60 +	80 +	80 +	60 +	40 +	.	.	.	.	.	20 r	40 +	.	.	20 r	.	.	.
Fraxinus excelsior - juv.	Fraexc	.	.	.	.	60 +	20 +	60 +	80 r	.	60 +	.	20 r	20 r	.	.	80 +	80 r	20 r	.	.	.	.
Rosa canina	Roscan	.	20 +	.	60 +	.	.	20 r	40 +	20 +	40 +	.	40 r	.	40 r	40 +	40 r	.	60 +	40 +	.	.	20 +
Polygala amarella	Polama	.	40 r	80 +	.	100 r	60 r	.	.	.	.	.	.	20 r	.	.	20 r	60 r	.	.	.	.	.
Cornus sanguinea	Corsan	.	.	.	.	40 +	100 +	80 +	.	20 +	40 1	.	.	.	.	40 +	20 +	20 +	.	.	80 1	.	40 +
Melilotus officinalis	Meloff	.	20 1	40 r	.	.	.	.	.	.	.	.	.	.	.	.	20 1	.	.	100 +	100 1	.	40 +
Acer campestre - juv.	Acecam	20 r	20 r	.	.	.	20 r	20 r	20 r	.	.	20 r	40 r	.	.	.	80 r	40 r	20 r	60 r	80 +	.	.
Galium verum	Galver	20 +	20 1	40 +	.	.	.	.	.	.	.	80 b	40 1	.	.	40 +	.	.	20 r	100 1	80 +	.	.
Ononis repens	Onorep	.	.	.	.	.	20 1	.	.	.	.	60 b	20 r	20 b	20 3	.	20 a	.	.	.	80 +	20 1	40 a
Senecio jacobea	Senjac	.	.	.	.	.	.	.	.	20 +	.	20 r	80 a	40 +	20 +	.	.	.	.	100 +	20 r	.	.
Trifolium repens	Trirep	.	20 r	.	.	.	.	.	.	.	.	80 +	80 +	20 +	20 +	.	.	.	.	20 +	.	40 +	.
Agrostis capillaris	Agrcap	.	.	.	.	.	.	.	.	.	.	80 a	40 +	60 +	60 +	.	.	.	.	20 +	.	20 +	.
Cirsium eriophorum	Cireri	.	.	.	.	.	.	.	.	.	.	100 +	60 +	20 +	80 +	.	.	.	.	.	.	.	.
Luzula campestris	Luzcam	.	.	.	.	.	.	.	.	.	.	100 +	40 r	60 +	20 r	.	.	.	.	.	.	20 r	.
Rhinanthus alectorolophus	Rhiale	.	.	.	.	.	.	.	.	.	.	40 r	60 a	80 r	.	.	20 +	.	.	.	.	.	.
Euphrasia sp.	Eupsp	.	.	.	.	.	20 r	.	.	.	.	20 1	20 r	60 +	60 +	40 r	.	.	.	.	.	.	.
Tragopogon dubium	Tradub	60 +	40 r	.	.	.	.	.	.	.	.	.	.	60 +	60 r	.	.	.	20 r	40 r	.	.	.
Arabis hirsuta	Arahir	.	.	.	.	.	.	.	20 r	.	.	.	.	60 r	20 r	.	.	.	.	.	20 r	20 1	60 1
Taraxacum sect. *Ruderalia*	Tarrud	20 +	20 r	.	.	20 r	.	.	.	40 r	.	60 +	40 +	100 +	.	40 r	20 r	20 r	.	20 r	.	.	20 +
Veronica teucryum	Verteu	.	20 r	.	.	.	40 r	20 r	.	.	20 r	.	.	.	.	20 r	.	.	.	40 r	60 r	60 1	.
Viburnum lantana	Viblan	.	.	.	.	80 1	60 +	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fragaria vesca	Fraves	.	.	.	.	.	40 r	20 +	.	20 +	20 r	.	20 +	40 r	.	.	20 +	.	.	.	.	.	.
Euphorbia verrucosa	Eupver	20 r	20 r	.	.	.	40 +	.	60 1	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.
Inula conyza	Inucon	.	.	.	.	.	20 r	.	.	.	40 +	.	.	.	.	.	.	.	80 r	.	20 +	.	.
Lathyrus pratensis	Latpra	.	.	.	.	.	20 r	.	.	.	.	20 +	40 +	.	.	.	40 r	.	.	.	40 r	.	.
Sorbus aria agg. - juv.	Sorari	.	40 r	.	.	.	80 r	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.	.
Carpinus betulus - juv.	Carbet	.	.	.	.	40 +	20 +	20 +	20 +	.	.	.	20 +	20 +	.	.	.	.	.	.	.	.	.
Quercus robur - juv.	Querob	.	.	.	20 r	20 r	.	20 +	.	20 +	20 +	.	.	.	.	.	.	20 +	.	.	.	.	.
Trifolium medium	Trimed	.	.	.	.	.	.	20 r	20 +	.	.	.	.	.	.	.	.	.	60 1	.	40 a	.	20 b
Potentilla reptans	Potrep	.	.	.	.	.	.	.	.	.	.	40 1	.	.	.	.	.	.	.	.	80 +	20 r	.
Cerastium arvense	Cerarv	.	.	.	.	.	.	.	.	.	.	20 +	40 r	40 +	.	.	.	.	.	.	.	40 +	.
Lolium perenne	Lolper	.	.	.	.	.	.	.	.	.	.	40 +	.	.	.	.	.	.	.	.	.	40 1	.
Trifolium campestre	Tricam	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	60 a	.
Arenaria serpyllifolia	Areser	.	.	.	.	.	.	.	.	.	.	.	.	20 +	.	.	.	.	.	.	.	80 +	20 1
Convolvulus arvensis	Conarv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	60 r	.	.	60 +	40 r
Melampyrum arvense	Melarv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 +	.	80 1
Primulla veris	Priver	.	.	.	.	.	40 +	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	40 +
Medicago sativa	Medsat	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	.	20 +	.	60 1
Rosa rubiginosa	Rosrub	.	.	.	.	.	40 r	20 +	.	.	40 +	.	.	.	.	.	.	.	.	.	.	.	.
Clematis vitalba	Clevit	.	.	.	.	.	.	40 r	.	.	20 1	.	.	.	.	.	.	.	20 +	.	.	.	20 +
Valeriana officinalis s.l.	Valoff	.	.	.	.	.	.	20 r	.	.	.	.	.	40 +	.	.	20 r	.	.	.	.	.	20 +
Gentiana verna	Genver	60 1	20 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Corylus avellana - juv.	Corave	.	.	.	.	20 +	20 +	.	.	.	.	.	20 +	20 +	.	.	.	.	.	.	.	.	.
Crataegus sp. - juv.	Crasp	.	.	.	.	.	60 +	.	.	.	.	.	.	.	20 r	.	.	.	.	.	.	.	.
Clinopodium vulgare	Clivul	.	.	.	.	.	20 +	.	.	.	.	.	40 +	.	.	.	.	.	.	.	20 r	.	.
Carex montana	Carmon	.	.	.	.	.	.	.	60 1	.	.	.	20 a	.	.	.	.	.	.	.	.	.	.
Phleum pratense	Phlpra	.	.	.	.	.	.	.	.	.	.	80 +	.	.	.	.	.	.	.	.	.	.	.
Coeloglossum viride	Coevir	.	60 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erigeron acris subsp. *acris*	Eriacr	.	.	.	40 +	.	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus sylvestris - juv.	Pinsyl	.	.	.	.	.	20 +	20 r	.	.	.	.	.	.	.	.	20 +	.	.	.	.	.	.
Picris hieracioides	Pichie	.	.	.	.	.	20 r	.	.	.	20 r	.	.	.	.	.	.	.	.	.	.	.	20 r
Ajuga genevensis	Ajugen	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	20 r	.	.	.	.	20 +	.	.
Allium oleraceum	Allole	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	60 r	.	.
Antennaria dioica	Antdio	20 b	.	.	20 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium murorum	Hiemur	.	.	.	.	20 +	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epipactis sp.	Episp	.	.	.	.	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.
Viburnum opulus	Vibopu	.	.	.	.	.	20 +	20 +	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis	Verarv	.	.	.	.	.	.	.	.	.	.	20 1	.	20 r	.	.	.	.	.	.	.	.	.
Leontodon autumnalis	Leoaut	.	.	.	.	.	.	.	.	.	.	40 r	.	.	.	.	.	.	.	.	.	.	.
Agropyron repens	Agrrep	.	.	.	.	.	.	.	.	.	.	20 +	20 +	.	.	.	.	.	.	.	.	.	.
Holcus lanatus	Hollan	.	.	.	.	.	.	.	.	.	.	20 +	.	.	20 r	.	.	.	.	.	.	.	.
Genista sagittalis	Gensag	.	.	.	.	.	.	.	.	.	.	.	.	.	40 +	.	.	.	.	.	.	.	.
Astragalus glycyphyllos	Astgly	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	.	20 r	.	.
Linaria vulgaris	Linvul	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r

Species in only one plot

Acer pseudoplatanus - juv. 14, *Campanula rapunculoides* 21, *Carduus nutans* 21, *Cirsium arvense* 4, *Echium vulgare* 1, *Gentianella ciliata* 2, *Geum urbanum* 4, *Listera ovata* 10, *Lonicera xylosteum* 14 , *Picea abies* - juv. 8, *Platanthera bifolia* 2, *Polygonum aviculare* subsp. *rurivagum* 11, *Potentilla erecta* 2, *Pulsatilla vulgaris* 19, *Ranunculus acris* 4, *Rubus idaeus* 4, *Salvia verticillata* 16, *Stachys alpina* 1, *Trifolium dubium* 15, *Triticum aestivum* 18, *Verbascum nigrum* 21.

Chapter 3

Identifying plant and environmental indicators of ancient and recent calcareous grasslands

Abstract

Dry calcareous grasslands are among the most species-rich habitats in Central Europe, harbouring numerous threatened species. Because of their strong decline, they are being protected under the European Habitats Directive. However, apart from this general decline, new grasslands developed after the abandonment of arable fields on marginal land over the course of the last few centuries or even decades.

The main question of this study was which species may indicate the age of a dry calcareous grassland habitat in the Franconian Jurassic mountains near Kallmünz. Furthermore, we asked if there is a general pattern of indicator species among available studies on ancient (i.e. those continuously used as pastures at least since 1830) and recent (i.e. those temporarily farmed as arable fields after 1830) calcareous grasslands. We compared the diversity parameters and nature conservation value of both grassland types. Additionally, we searched for differences in habitat and soil parameters.

We compiled a list of indicator species of both ancient and recent grasslands in the study region. Comparison with other studies leads to the conclusion that there are not many species that clearly indicate grassland age across different regions (the best indicators are *Carex caryophyllea*, *Cirsium acaul*e and *Hippocrepis comosa* for ancient grasslands, and *Agrimonia eupatoria* and *Astragalus glyciplyllos* for recent grasslands).

Ancient grasslands harbour a somewhat greater number of threatened species than recent grasslands. Many species of the ancient grasslands under study can be considered relict species of steppic grasslands or open pine forests (e.g. *Hippocrepis comosa*, *Pulsatilla vulgaris*, *Teucrium chamaedrys*, *Teucrium montanum* and *Thymus praecox*). Recent grasslands also harbour rare and endangered species, especially disturbance-tolerant relicts of former arable use (e.g. *Melampyrum arvense*) and may therefore be of high conservation value, too.

The average number of species per plot is greater in ancient grasslands. However, the most species-rich plot (46 species of vascular plants within a 4-m^2 quadrat) was found in a 60 years old grassland.

Arable cultivation in the past has altered the physical and chemical properties of the soil of recent grasslands. In general, ancient grasslands occur on nutrient-poorer and less calcium-rich soils with high water holding capacity. High water holding capacity is connected with high humus content, which increases the importance of ancient grasslands for carbon storage.

The challenges and benefits of differentiating grasslands of different age in the management of protected areas and landscape planning (e.g. the identification of High Nature Value farmland) are discussed.

Keywords: Biodiversity; Conservation value; Dry grassland vegetation; Land use indicators; Soil properties; Species richness

Introduction

Dry calcareous grasslands are, because of their high species diversity and the occurrence of many rare species, valued as one of the most important habitats in Europe from a conservation point of view (e.g. Korneck et al. 1998, Wallis de Vries et al. 2002, Sádlo et al. 2007). They are therefore listed in Annex I to the European Natura 2000 Habitats Directive (92/43/EEC). However, dry calcareous grasslands may strongly differ in their floristic composition, which may depend not only on habitat quality and management, either by grazing or by mowing, but also on their age (Karlík & Poschlod 2009). Relict grasslands, which are limited to areas with extreme conditions, deserve special attention because they have survived in Central Europe in direct continuity with post-glacial cold continental steppes and have been maintained by humans since the beginning of settlement (Pokorný et al. 2015). By contrast, semi-natural grasslands, which are the subject of the present study, represent secondary vegetation developed from forests, often as a consequence of forest grazing. Such grasslands have been proven to exist since the Neolithic (Kaligarič et al. 2006, Dutoit et al. 2009, Poschlod & Baumann 2010, Hájková et al. 2011, Robin et al. 2018) or to have been created during later stages of agricultural colonization. Species of semi-natural grasslands may have survived either in open forests (Roleček et al. 2014) or in microrefugia (Bylebyl et al. 2008, Tausch et al. 2017). Many, however, immigrated into Central Europe with the first settlers and their livestock (Poschlod 2015b, Meindl et al. 2016, Leipold et al. 2017).

When considering the historical perspective of grassland sites, a distinction is often drawn between ancient and recent grasslands. Ancient grasslands are at least one or two centuries old, as evidenced by the first detailed information contained in cadastral maps (Gibson & Brown 1991, Karlík & Poschlod 2009). By contrast, recent grasslands originated through succession on former arable land since the middle of the 19th century, when new agricultural techniques were developed, resulting in increased production (Hard 1964, Baumann et al. 2005, Mailänder 2005). Large areas of new semi-natural grasslands developed only over the 20th century on less agriculturally favourable land. Arable farming on marginal land was abandoned because of socio-economic and political changes (e.g. Osbornová et al. 1990, Ruprecht 2005, Illyés & Bölöni 2007, Chýlová & Münzbergová 2008, Poschlod et al. 2008). The establishment of military training estates was another reason why recent grasslands developed on former fields (Wells et al. 1976, Redhead et al. 2014).

Concurrently with the growing extent of new semi-natural grasslands developing on former arable land, the area of ancient grasslands decreased significantly from the end of the 19th century onwards (Quinger et al. 1994), and the strongest decline took place during the 1960s and 1970s (Mattern et al. 1992, Wallis de Vries et al. 2002, Mauk 2005) because of altered farming practices and decline of sheep numbers (Poschlod & Wallis DeVries 2002, Baumann et al. 2005). Numerous localities of high conservation value have overgrown with shrubs. Today, there are strong efforts to restore at least part of these localities (Bylebyl 2007, Calaciura & Spinelli 2008, Dostálek & Frantík 2008, Piqueray et al. 2011, Rákosy & Schmitt 2011, Piqueray et al. 2015).

Ancient and recent grasslands can differ in many features: their biodiversity, number of endangered species and also the value of ecosystem services they provide. Therefore, a deeper understanding of these differences might prove useful not only in nature conservation, but also in agriculture and landscape management (Gustavsson 2007). Maintenance of conservationally valuable grasslands on a larger scale in the conditions of the European Union is achievable only with some suitable mechanism under the Common Agricultural Policy. One suitable approach is the concept of so-called High Nature Value (HNV) farmland, where semi-natural grasslands are regarded as the core of European HNV farmland (Oppermann et al. 2012).

The most essential source of information for researching the history of land use are records in archives and old maps, which have been available in sufficient resolution and precision since the second half of the 18th century, and especially since the first half of the 19th century in Central Europe (Baumann et al. 2005, Mailänder 2005, Haase et al. 2007, Skaloš et al. 2011). In parallel, land use history may also be reflected by indicator species. They are especially useful for cross-validation or in regions, for times and on spatial scales for which maps are unreliable or not available. Studies dealing with species composition and identifying species that indicate ancient and recent grasslands are quite rare (e.g. Gibson & Brown 1991, Ejrnæs & Bruun 1995, Chýlová & Münzbergová 2008, Karlík & Poschlod 2009, Forey & Dutoit 2012, Schmid et al. 2017). So far, however, there is no comparison or synthesis. Furthermore, there is the question whether it is possible to find species with sufficiently strong indicator ability and validity across regions, which has until now been asked only about recent and ancient forests (e.g. Peterken & Game 1984). Some of these forest indicators are useful in general, but others are useful only in certain regions. Differences in indicator species turn out to be caused by the climate, geology and pedology, a unique history of management, biogeographic gradients, and the type of sources used to assess the history of land use (e.g. Graae 2000).

We therefore addressed the following questions:

- Is it possible to identify plant indicators of ancient and recent grasslands in the study region of Kallmünz in the Franconian Alb?
- What are the differences between ancient and recent calcareous grasslands in soil physics and chemistry in the study region?
- Do indicator species of ancient and of recent grasslands differ between regions?
- What is the nature conservation value of ancient grasslands compared with that of recent ones?

Material and Methods

Study area

The study area is situated in the German part of the Jurassic mountains, the Franconian Alb near the small town of Kallmünz (Bavaria, Upper Palatinate). Kallmünz is situated ca. 20 km north-east of the city of Regensburg at the confluence of the rivers Naab and Vils (Fig. 3.1).

Its altitudes range from 340 to 440 m above sea level. The climate is temperate, with the mean annual precipitation of 649 mm and a mean annual temperature of 7.8°C. It can be called slightly sub-continental.

The bedrock of the study area is of the so-called Malm type, an upper Jurassic formation consisting mainly of solid and hard reef limestone. Scattered in elevated places are younger Cretaceous sandstones (Müller 1961, Meyer & Schmidt-Kaler 1995).

The main soil type is Rendzina, partly developed as brown soil. Soils are mainly very shallow and contain a high proportion of dolomitic sand.

The oldest archaeological findings date back to the Neolithic period and are situated on a floodplain. An ancient hillfort from the Bronze and La Tène Ages is situated on the plateau above the river confluence and is said to be one of the largest prehistoric settlements in Bavaria. A medieval castle was built in the same place. The first historical record of the town Kallmünz is dated 990 AD (Frisch 1998, Sandner 2005).

The vegetation of dry grasslands near Kallmünz was studied in detail by Sendtko (1993). Most of them belong to the typical association of southern German calcareous grasslands – *Gentiano-Koelerietum* (alliance *Mesobromion*) and various initial or degraded stages of this association.

Because of their large extent and high conservation value, the dry grasslands near Kallmünz have been included in the European Natura 2000 network under the Habitats Directive 92/43/EEC (site code and site name: 6838-301 Dry slopes at Kallmünz).

Calcareous grasslands of the study sites have been used as pastures. There is no indication that haymaking was practised elsewhere than on the floodplain. Besides the grazing of cattle and other domestic livestock, sheep grazing, practised mainly as the so-called South-German transhumance, was greatly important (Hornberger 1959, Poschlod & Wallis de Vries 2002).

Grazing ceased at the end of the 1960s. It was re-introduced since 1985 due to the high conservation value of the study region. Since 2001 the majority of the surveyed plots have been regularly grazed by sheep and sometimes shrubs were removed.

A significant part of the current calcareous grasslands had been used as arable fields in the past. They were converted into grasslands in different times and for different reasons (new farming methods, socio-economic changes). The area of dry grasslands increased until the 1960s. From the 1960s onwards, the area of calcareous grasslands has declined significantly because of the cessation of grazing and subsequent succession of woody species or due to intentional afforestation. Nevertheless, the study region covers the large proportion of grasslands that are still maintained (Baumann et al. 2005, Poschlod et al. 2008).

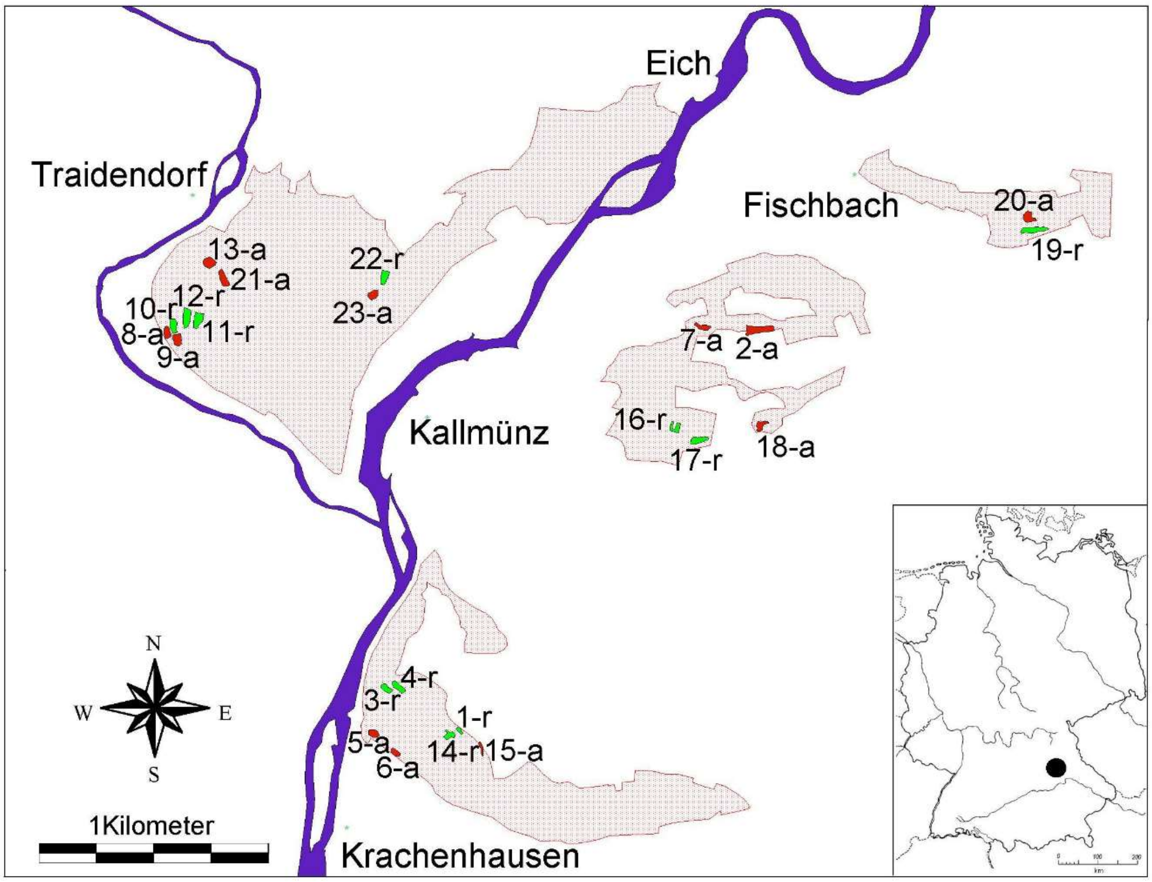

Fig. 3.1. – Locations of investigated ancient (dark grey/red, 'a') and recent (grey/green, 'r') grasslands in the study area. The inset shows the position of the Kallmünz region in Germany. Bright grey areas represent 'Special Area of Conservation' according to the European Natura 2000 network (site code and site name: 6838-301 Dry slopes at Kallmünz). The rivers Naab and Vils and the positions of settlements are charted.

Study sites

The grasslands analysed in this study were selected using cadastre maps from 1830 onwards. Grasslands were considered ancient when they had been continuously managed as pastures at least since 1830, but often even since the Roman period (Baumann 2006, Poschlod & Baumann 2010). Considered recent were those grasslands which were marked as arable land at least on the first cadastre maps from 1830. Their age was reconstructed using cadastre maps from after 1830, cadastre books from the 1960s, aerial photographs from 1988 onwards, or by interviewing old local people. A small part of recent grasslands developed before World War II. The area of recent grasslands increased significantly a few years after World War II when the economic situation improved and self-supply farming lost its importance. Other recent grasslands were established in the 1970s or early 1980s due to agricultural intensification connected with the abandonment of arable farming on less suitable land. The youngest grassland included in this study was approximately 15 years old (at the time of our botanical survey). For some analyses we differentiated two recent grassland age categories: older than 50 years (five sites) and younger than 50 years (six sites).

In total, we selected twelve ancient and eleven recent grasslands. The selection of ancient and recent grasslands followed the criteria that environmental characteristics such as slope, aspect and soil depth should differ as little as possible between the grassland categories.

Vegetation data collection

Vegetation was recorded during June-September in the growing seasons of 2005 and 2006. Five 4-m^2 plots were placed semi-randomly (with the exclusion of rocky, overgrown or strongly disturbed patches) in each of the selected grasslands and surveyed as phytosociological relevés using Braun-Blanquet's nine-degree abundance-dominance scale (Barkman et al. 1964). For each plot we calculated species diversity using the number of species (species richness) and the Shannon-Wiener index. The Shannon-Wiener index of diversity (Begon et al. 1990) was calculated in CANO-DRAW (ter Braak & Šmilauer 2002).

In a few cases, when young plants without flowers occurred, we did not make precise determinations to the species level and merged them into collective taxa. This applies to *Platanthera* sp. (probably *P. bifolia*), *Vicia cracca* agg. (including *V. tenuifolia*, which probably prevails) and *Vicia sativa* s.l. (*V. angustifolia* s.str. occurs at least in some plots).

From further analyses we omitted seedlings and juveniles of trees and shrubs. The dataset included 12 such species that mostly occurred only rarely and with low cover. In total, 161 taxa were included in the analysis. A summary table of the dataset is provided in Appendix 3.1. The nomenclature follows Rothmaler (2005) for species and Oberdorfer (2001) for syntaxa. For table sorting and some analyses, we used diagnostic species of the alliances *Bromion* and *Arrhenatherion* following Lang & Walentowski (2010) and the Red List of Bavaria assembled by Scheuerer & Ahlmer (2003).

Environmental data collection

On every plot a set of environmental parameters was collected. This included altitude, slope inclination, slope aspect, cover of the herb- and moss-layer, cover of stones, occurrence of ant-hills (y/n) and soil parameters. Furthermore, data on latitude, slope inclination and aspect were used to calculate potential direct solar irradiation (PDSI). The calculation was done on the twenty-first day of each month between December and June following the recommendations of Jeník & Rejmánek (1969). The following soil physical and chemical parameters were measured for each plot: soil depth, water holding capacity (WHC), pH_{H2O}, conductivity, and potassium (K) and phosphorus (P) content. For every plot, the two following soil variables were noted: colour of soil (four classes) and fragments of ceramics (presence of sherds, bricks, roof tiles, etc. in approx. 0.75-L soil samples). Furthermore, two samples from every site were analysed for N_{total} (%), C_{total} (%) and $C_{carbonate}$ (%), from which the $C_{organic}$: N ratio was derived.

Soil depth was estimated by repeated sticking a 0.6 cm thick iron rod into the soil (in 8 places per plot). Water-holding capacity was measured by collecting soil monoliths using metal cylinders with a standardized volume of 100 cm^3 (diameter 56.4 mm, height 40 mm). After being collected, the soil monoliths within cylinders were saturated with water by standing on a constantly wet sheet of filter paper. Afterwards, the water-saturated samples were dried at 105°C until constant weight. Water-holding capacity was calculated using the following formula: WHC = (weight of water saturated soil – weight of dry soil) × 100 / weight of dry soil.

For the measurement of soil chemical and physical parameters, soil from the depth of 5 to 10 cm was collected at three points within each plot and mixed afterwards. The soil was air-dried and sieved through a 2 mm sieve before the analysis.

Soil reaction (pH) was measured in a 1:2.5 suspension of dry soil and distilled water (active soil acidity) after 1 hour using a universal pH meter WTW SenTix41. Conductivity was analysed in a 1:5 suspension of dry soil and distilled water with a WTW LF340 apparatus. Plant-available P and K were extracted by calcium acetate lactate (CAL). Phosphorus was measured photometrically after making the P content visible with ammonium heptamolybdate. K was analysed with an atomic absorption spectrometer.

Total C and N contents were determined using a Carlo Erba NC 2500 CHN elemental analyser. Because the soils were calcareous, it was necessary to measure the content of $C_{carbonate}$, which was done using the volumetric method based on the reaction with HCl. After the subtraction of anorganic carbon from C_{total} we obtained $C_{organic}$.

To filter out any possible effects of the spatial distribution of samples, geographic coordinates of sampling plots (in the Gauß-Krüger coordinate system) and their combinations were included in the analysis (Fortin & Dale 2009).

In general, the data were calculated for the number of 115 samples (ancient: n=60; recent: n=55). Only data about N and C content, where two soil samples from each site were analysed, were calculated based on a total of 46 samples (ancient: n=24; recent: n=22).

<u>*Data analysis*</u>

Indicator species for both ancient and recent grasslands can be detected by a range of methods that offer similar results. In this paper, we present only the results of calculations of fidelity expressed as the Phi-coefficient (Sokal & Rohlf 1995, Chytrý et al. 2002). Data were processed using JUICE 7.0 (Tichý 2002).

Differences in environmental parameters between ancient and recent grasslands were analysed by applying the Student t-test if the data had a normal distribution or using the Mann-Whitney U-test if the data had non-normal distribution. Because of the high variability of recent grasslands, they were further differentiated into 'older recent' (>50 years old) and 'younger recent' (<50 years old) ones. These three grassland age classes (ancient, >50 years old and <50 years old) were analysed using one-way ANOVA and its non-parametric counterpart, the Kruskall-Wallis test. Using HSD post-hoc test for unequal N, differences between particular grassland age categories were ascertained. All these analyses were done in Statistica 12 (www.statsoft.com).

Ordination techniques were applied to identify differences between the vegetation of ancient and recent grasslands and the influence of environmental factors. Methods based on linear species responses were chosen. This was supported by the fact that the dataset included only one vegetation type (dry grassland) recorded in a relatively small region and by the rather short length of the gradient in the DCA analysis, which took 3.6 S.D. units. Thus, principal components analysis (PCA) and its constrained counterpart, redundancy analysis (RDA) were applied using CANOCO for Windows 4.5 (ter Braak & Šmilauer 2002).

To estimate the influence of environmental factors, the eigenvalues of the corresponding ordination axes from unconstrained (PCA) and constrained (RDA) analyses were compared (Šmilauer & Lepš 2014). The scaling is focused on inter-species correlations to improve the visibility of species' positions in biplots. Species scores were divided by the standard deviation. Species coverages (in percentages), unless instructed otherwise, were transformed using the formula y= (ln x + 1). Neither centring nor standardization were used for samples (vegetation plots). Centring, but not standardization, was used for species. The statistical significance of all canonical axes in RDA's was determined using Monte Carlo permutation tests with 1,999 permutations and a reduced model. The permutations were restricted to the split-plot design. We used only one explanatory variable in the main analysis: grassland history. The remaining variables were used as covariables in the RDA in order to filter out different environmental variables and spatial gradients and to single out the effect of history on species composition. The significance of all potential covariables was at first tested by manual forward selection ($p = 0.05$; Monte Carlo test, 499 permutations). The following ten environmental variables were selected by the above mentioned forward-selection function: cover of the herb layer, cover of the moss layer, grazing, number of species, phosphorus content, water holding capacity, altitude, PDSI on 21 December, and geographic coordinates X and Y.

To ascertain the extent to which the indicator species of historical status of grasslands found in our work are transferable to other regions, we searched the literature on semi-natural dry grasslands in different regions of Europe. We omitted articles that lack a clear definition of ancient grasslands or that do not present primary data. We found 12 usable studies (Cornish 1954, Wells et al. 1976, Gibson & Brown 1991, Ejrnæs & Bruun 1995, Ejrnæs et al. 2008, Fagan et al. 2008, Chýlová & Münzbergová 2008, Karlík & Malíček 2008, Karlík & Poschlod 2009, Forey & Dutoit 2012, Redhead et al. 2014, Schmid et al. 2017) listing indicator species of ancient and recent (>10 years old) grasslands, from which we compiled a table. We classified the indicator ability of indicator species into six ad hoc defined semi-quantitative categories representing low, moderate and high indication ability for each of the two grassland types. Whilst these did not share an exact definition across the aforementioned studies due to their different extents, experimental designs, analytical methods and ways they present data, the main criteria were exclusivity (i.e. whether a species grows only in ancient or only in recent grasslands) and the frequency of indicator species, weighted by the number and size of the vegetation samples under study.

Results

<u>Assessment of indicator species</u>

Table 3.1 presents indicator species of ancient and recent grasslands, identified based on significant values of fidelity to the former or latter sample group. The best indicator species of ancient grasslands with highest fidelity (Phi-coefficient > 50) were *Asperula cynanchica*, *Carex caryophyllea*, *Chamaecytisus ratisbonensis*, *Helianthemum nummularium* s.l., *Potentilla neumanniana*, *Prunella grandiflora*, *Salvia pratensis* and *Teucrium chamaedrys*. All these species were very frequent in ancient grassland plots, often being the dominants or subdominants of the vegetation.

The best indicator species for recent grasslands (Phi-coefficient > 40) were *Agrimonia eupatoria*, *Arrhenatherum elatius*, *Daucus carota* and leguminous species such as *Medicago* *lupulina*, *Vicia cracca* agg., *Vicia hirsuta* and *Vicia sativa* s.l. Some of them were dominant in the vegetation, especially *Arrhenatherum elatius*, *Agrimonia eupatoria* and *Medicago lupulina*. However, the frequency of species indicating recent grasslands in the dataset was on the whole lower than the frequency of ancient species (Table 3.1, Appendix 3.1).

Notable is the fact that the number of identified indicator species in the two grassland types is similar (44 indicator species of ancient grasslands and 40 species of recent grasslands).

A critical evaluation of the usability of grassland age indicators is presented in Fig. 3.2. We can state that ancient grasslands are characterized by the occurrence of at least 27 ancient indicator species and less than 13 indicators of recent grasslands. At least nine indicators of recent age and no more than 29 indicators of ancient age grow in recent grasslands. The overlapping values between ancient and recent grasslands were mainly caused by specific older recent grasslands.

Occurrence of endangered and diagnostic species

In general, more threatened species were present in ancient than in recent grasslands (Table 3.2). Many threatened species typical of ancient grasslands were quite common in the sample plots (e.g. *Chamaecytisus ratisbonensis*, *Genista sagittalis*, *Globularia bisnagarica* and *Pulsatilla vulgaris*). On the other hand, the only endangered species commonly present in recent grasslands was *Melampyrum arvense*. Other threatened species occurring exclusively in recent grasslands were not frequent and grew in only one or two plots (*Arabis glabra*, *Cynoglossum officinale*, *Muscari comosum*, *Petrorhagia prolifera*, *Silene otites*, *Veronica teucrium*) (Appendix 3.1).

The total number of species was greater in recent grasslands (Table 3.2), but the average number of species per plot was greater in ancient plots (Table 3.3).

In both types of grasslands, numerous diagnostic species from the phytosociological alliances *Bromion* (40 species altogether in ancient and recent grasslands) and *Arrhenatherion* (29 species) occur. In both grassland categories a similar number of phytosociological diagnostic species (59 species in ancient and 60 in recent grasslands respectively) was found, but the proportion of species of individual alliances differed. In ancient grasslands, the number of diagnostic species of the *Bromion* alliance prevailed over *Arrhenatherion* species, whereas in recent grasslands the ratio of *Bromion* to *Arrhenatherion* species was nearly equal. An even greater difference was found in the variable 'frequency of occurrences', which revealed that numerous diagnostic species of the *Bromion* alliance grew abundantly in ancient grasslands. By contrast, many diagnostic species of the *Arrhenatherion* alliance occurred only sparsely and with rather low coverage in the dataset (Table 3.2, Appendix 3.1).

Table 3.1. – Summary of indicator species of both ancient and recent grasslands based on 4-m2 plots. Species are sorted by their fidelity expressed in terms of the Phi-coefficient (using presence/absence data; calculated by JUICE 7.0; Tichý 2002). Only species with significant fidelity to each group are listed (P = 0.05; Fisher's exact test). Highly significant species (P = 0.001; Fisher's exact test) are highlighted in bold. The number of plots is 60 for ancient and 55 for recent grasslands. Percentage frequencies of each species in each group are given.

Indicators of ancient grasslands

Species	fidelity ancient	fidelity recent	frequency (%), ancient	frequency (%), recent
Teucrium chamaedrys	87.8	---	93	5
Carex caryophyllea	82.7	---	95	13
Helianthemum nummularium s.l.	71.5	---	78	7
Prunella grandiflora	66.1	---	70	5
Salvia pratensis	63.6	---	80	16
Chamaecytisus ratisbonensis	58.4	---	68	11
Asperula cynanchica	54.8	---	67	13
Potentilla neumanniana	52.3	---	88	38
Teucrium montanum	49.2	---	40	.
Pulsatilla vulgaris	48.2	---	52	7
Avenula pratensis	48.1	---	97	56
Thymus praecox	46.7	---	60	15
Brachypodium pinnatum	46.6	---	97	58
Luzula campestris	46.6	---	37	.
Cerastium arvense	45.1	---	53	11
Dianthus carthusianorum	44.2	---	78	35
Hippocrepis comosa	43.6	---	43	5
Sanguisorba minor	42.6	---	80	38
Briza media	42.5	---	72	29
Koeleria pyramidata	42.4	---	95	60
Phleum phleoides	41	---	88	51
Euphorbia cyparissias	40.8	---	95	62
Anthyllis vulneraria	40	---	45	9
Potentilla cinerea	38.1	---	40	7
Cirsum acaule	36.1	---	43	11
Potentilla x *subarenaria*	35	---	27	2
Anthericum ramosum	34.2	---	22	.
Genista sagittalis	34.2	---	22	.
Globularia bisnagarica	32.7	---	20	.
Sesleria albicans	32.7	---	20	.
Ranunculus bulbosus	31.3	---	58	27
Bromus erectus	28.4	---	35	11
Peucedanum oreoselinum	24.4	---	12	.
Polygala chamaebuxus	24.4	---	12	.
Arenaria serpyllifolia	23.8	---	25	7
Trifolium montanum	23.5	---	30	11
Orchis morio	22.5	---	10	.
Campanula rotundifolia	21.8	---	28	11
Carex flacca	21.3	---	17	4
Ajuga genevensis	20.4	---	8	.
Galium pumilum	20.4	---	8	.
Pimpinella saxifraga	19.7	---	65	45
Medicago falcata	19.4	---	50	31
Linum catharticum	19.1	---	42	24

Indicators of recent grasslands

Species	fidelity ancient	fidelity recent	frequency (%), ancient	frequency (%), recent
Arrhenatherum elatius	---	61.7	7	65
Vicia hirsuta	---	57.9	.	49
Agrimonia eupatoria	---	54.1	3	51
Vicia cracca agg.	---	46.4	2	38
Vicia sativa s.l.	---	43.5	.	31
Medicago lupulina	---	42.5	28	71
Daucus carota	---	41.8	2	33
Falcaria vulgaris	---	38.6	2	29
Trifolium campestre	---	38.3	10	44
Melampyrum arvense	---	37.3	.	24
Veronica chamaedrys	---	37.1	3	31
Veronica arvensis	---	35.7	.	22
Knautia arvensis	---	35.5	23	58
Galium mollugo s.l.	---	34	.	20
Potentilla reptans	---	34	.	20
Campanula rapunculoides	---	32.2	.	18
Dactylis glomerata	---	31.3	17	45
Securigera varia	---	30.9	65	91
Agropyron repens	---	30.4	.	16
Plantago lanceolata	---	30.3	23	53
Cerastium pumillum agg.	---	30.1	3	24
Festuca pratensis	---	30	2	20
Lathyrus pratensis	---	30	2	20
Leucanthemum vulgare	---	30	2	20
Rhinanthus minor	---	30	2	20
Fragaria viridis	---	27.3	40	67
Valerianella locusta	---	26.6	.	13
Taraxacum sect. *Ruderalia*	---	24.9	33	58
Cerastium holosteoides	---	24.5	.	11
Festuca rubra	---	24.5	.	11
Anthriscus sylvestris	---	24.5	.	11
Tragopogon dubium	---	24	2	15
Trisetum flavescens	---	24	2	15
Senecio jacobaea	---	23.9	7	24
Astragalus glyciphyllos	---	22.3	.	9
Myosotis stricta	---	22.3	.	9
Sedum acre	---	22.3	.	9
Silene vulgaris	---	22.3	.	9
Achillea millefolium	---	21.3	83	96
Trifolium medium	---	19.8	.	7

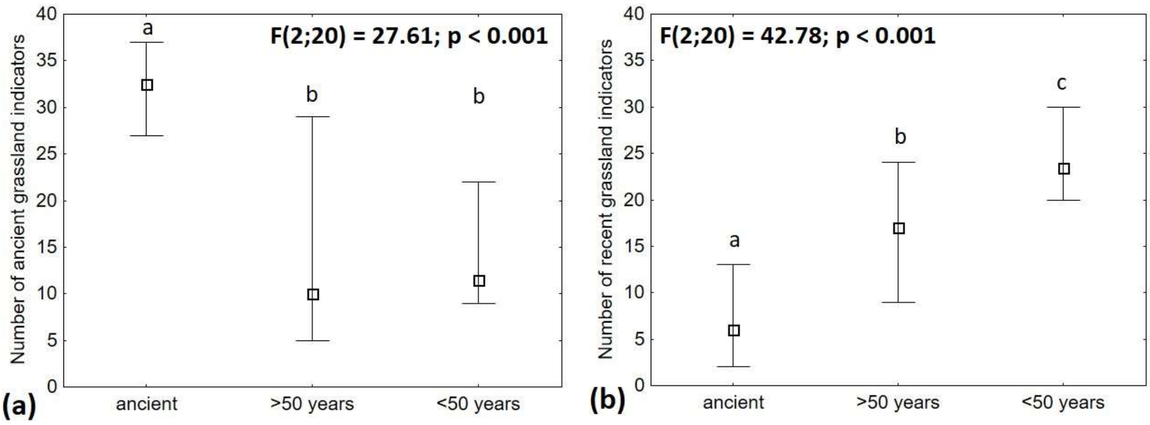

Fig. 3.2. – Numbers of indicator species of ancient (a) and recent (b) grasslands within three grassland age classes (ancient, >50 years old and <50 years old). Whiskers show minimum and maximum, and squares indicate median values. Different letters indicate significant differences between particular grassland age categories revealed using HSD post-hoc test for unequal N.

Environmental variables

Nearly all measured environmental variables differed significantly if the samples were divided according to grassland age (Table 3.3). To extract more information from the data, we divided the grasslands not into two (ancient versus recent) but into three age groups (Fig. 3.3). Correlations between particular variables are apparent from Fig. 3.4.

In general, ancient grasslands occurred on nutrient-poorer and less calcium-rich soils with high WHC. Ancient grasslands were situated on steeper slopes than recent grasslands. However, this difference turned out to be of little importance for insolation (solar radiation reaching the grassland surface). The largest difference in solar irradiation (PDSI) between grassland age categories was ascertained in December, but there was no significant difference between ancient and older recent grasslands. Ancient grasslands were characterized by the absence of ceramic fragments in the soil. Younger recent grasslands (<50 years) had an enhanced cover of the herb layer; however, there was no difference between ancient and older recent (>50 years) grasslands. Ancient grasslands had a greater cover of stones, with lowest values in older recent grasslands, but the actual values were always low. Larger differences were present in the cover of the moss layer, which was the largest in ancient grasslands and the smallest in younger recent grasslands. Older recent grasslands (>50 years) were characterized by intermediate values of most variables. In the case younger recent grasslands (<50 years), typical attributes were a deeper soil profile, high pH, high phosphorus content, low humus content indicated by low $C_{organic}$, low WHC and bright soil colour.

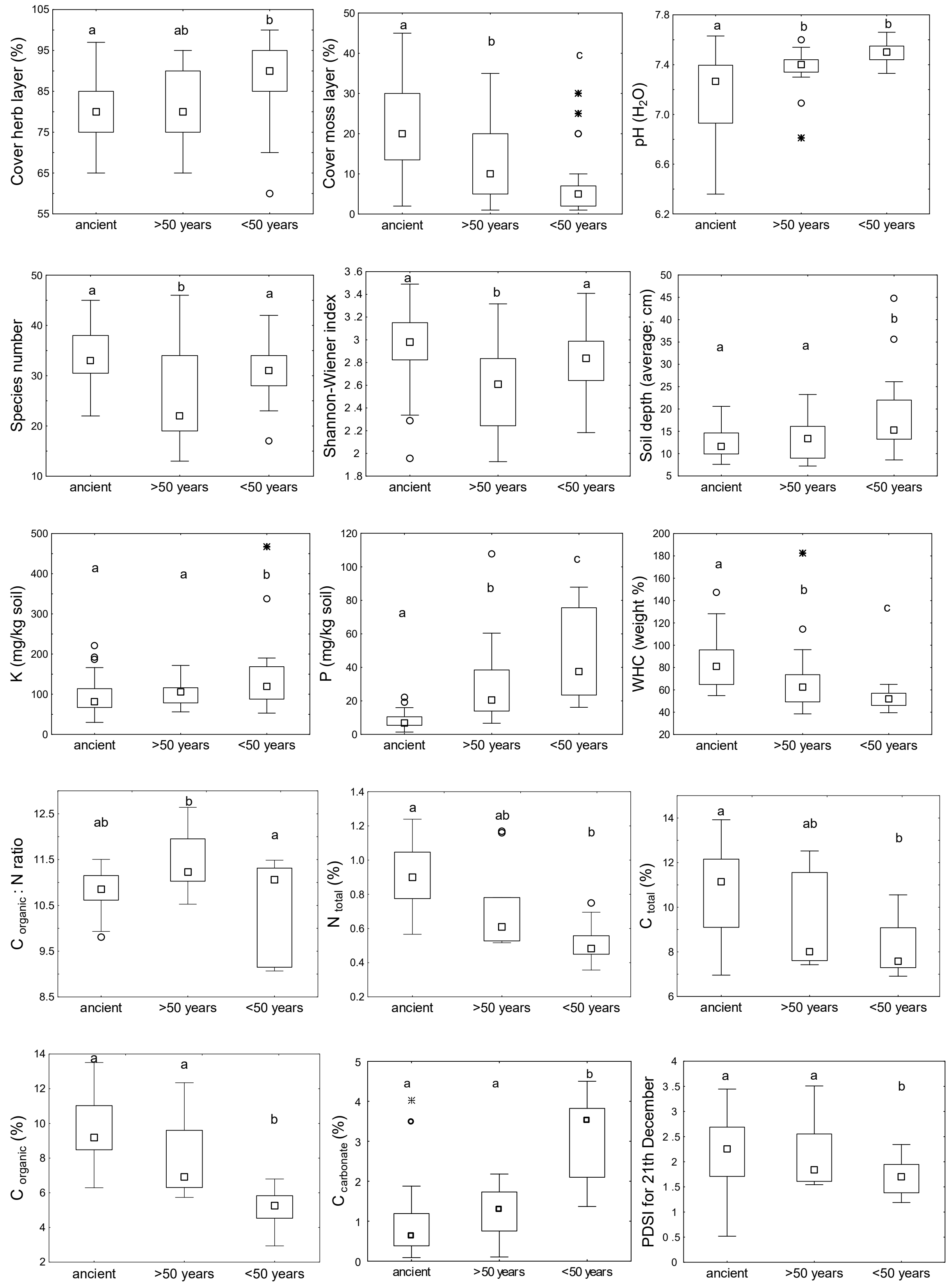

Fig. 3.3. – Selected environmental variables within three grassland age classes (ancient, >50 years old and <50 years old). Different letters indicate significant differences between particular grassland age categories revealed using HSD post-hoc test for unequal N. Boxes represent the first and third quartiles; whiskers show the non-outlier range, squares indicate median values, circles mark outliers, and asterisks represent extreme values.

Table 3.2. – Numbers and frequencies of species indicating the nature conservation status of grasslands studied. Diagnostic species of the alliances *Bromion* and *Arrhenatherion* according to Lang & Walentowski (2010); Red List of Bavaria (Scheuerer & Ahlmer 2003) divided into four categories (Red List 1, Red List 2, Red List 3 and 'early warning'); § – protected species according to the German Federal Directive.
The numbers of threatened and diagnostic species were calculated with the exclusion of trees and shrubs (there was only one important woody species, *Juniperus communis*, which belongs to the 'early warning' category according to the Red List).

	All relevés (N=115)		**Ancient (N=60)**		**Recent (N=55)**	
	Number of species	Number of occurrences	Number of species	Number of occurrences	Number of species	Number of occurrences
Number of species-including trees and shrubs	173	3594	119	2028	145	1566
Number of species-without trees and shrubs	161	3541	111	2011	138	1529
Bromion	40	1480	39	1080	31	400
Arrhenatherion	29	715	20	247	29	468
RL1	0	0	0	0	0	0
RL2	4	12	2	9	3	3
RL3	19	228	16	165	12	63
Early Warning	34	752	29	526	24	226
§	8	82	7	70	4	12
RL1 + RL2 + RL3	23	240	18	174	15	66
RL incl. Early Warning	57	992	47	700	39	292
RL + Early Warning + §	58	994	48	702	39	292

Table 3.3. – Values of environmental variables for ancient and recent grasslands based on 4-m^2 plots and represented by means and standard deviations (SD) for both groups. Results of t-tests, and non-parametric U-tests and their significance values (p) are shown.
Most values were calculated for the number of 115 samples (ancient: n=60; recent: n=55). Only values concerning N and C content are based on 46 samples (ancient: n=24; recent: n=22).

Variable	Ancient		Recent		Test results		
	Mean	SD	Mean	SD	t	U	p
Slope aspect (°)	206.63	66.55	204.82	72.55		1566	0.638
Slope inclination (°)	11.52	5.58	6.60	5.26		837	<0.001
Cover herb layer (%)	80.30	8.89	84.60	9.17	2.55		0.012
Cover moss layer (%)	20.90	10.83	9.98	9.64		721	<0.001
Cover of stones (%)	0.47	0.75	0.16	0.71		1246	0.024
Soil depth (average; cm)	12.50	3.42	15.85	6.77	3.39		0.001
Soil depth (median; cm)	12.04	3.51	15.34	7.10	3.20		0.002
Species number	33.82	5.60	28.49	7.88	-4.20		<0.001
pH $_{H2O}$	7.16	0.33	7.44	0.13		710	<0.001
Conductivity (μS)	147.70	50.54	131.56	23.97		1425	0.209
P (mg/kg soil)	8.01	3.84	38.11	25.28		142	<0.001
K (mg/kg soil)	92.39	37.42	121.84	67.34		1109	0.002
WHC (weight %)	83.67	21.07	59.04	22.11		449	<0.001
Color of soil	3.16	0.37	2.55	0.61		755	<0.001
N_{total} (%)	0.89	0.19	0.61	0.21	-4.83		<0.001
C_{total} (%)	10.63	2.04	8.77	1.79		123	0.002
$C_{carbonate}$ (%)	0.98	0.96	2.15	1.29		102	<0.001
$C_{organic}$ (%)	9.65	2.10	6.68	2.28	-4.56		<0.001
$C_{organic}$: N ratio	10.82	0.44	11.01	0.94	0.88		0.385
Pieces of broken pottery	0.00	0.00	0.07	0.26		1530	0.503
Fragments of ceramic	0.03	0.18	0.51	0.50		865	<0.001
Altitude (m a.s.l.)	389.17	24.60	392.73	17.13		1263	0.030
PDSI 21. December	2.19	0.71	1.88	0.54	-2.57		0.011
Shannon-Wiener Index	2.96	0.28	2.71	0.35	-4.31		<0.001
X	4497241	1181.011	4497190	1088.556		1648	0.991
Y	5447320	850.446	5447099	835.784		1521	0.472

Multivariate direct analyses

The results show that history is definitely the most important factor affecting the actual vegetation pattern (explaining 15.6 % of the variability in the data, Table 3.4). However, other variables are also important, especially those pertaining to soil properties, above all plant-available P (12.5%) and WHC (7.4%), but also vegetation cover (the moss layer explains 10.7% of data variability).

The results also show that three age categories (ancient, older recent, younger recent) describe vegetation more precisely, explaining 19.0 % of variability in the data, in contrast to two categories (ancient and recent), which explained only 15.6%. The pure effect of history after the subtraction of covariables is quite high with 7.8 % of explained variability if we used three age groups (and 5.2 %

in the case of two age categories). Furthermore, results of the Monte Carlo permutation test are highly significant (Table 3.4).

The values mentioned above were calculated using log-transformed species cover data. Presence-absence data explained a little less variability. Analysis of untransformed data found history to explain only half of the variability (8.1%) compared to that of transformed data. This indicates that species with low abundance are on the whole a more important source of information about the history of grasslands under study than the limited group of dominant species.

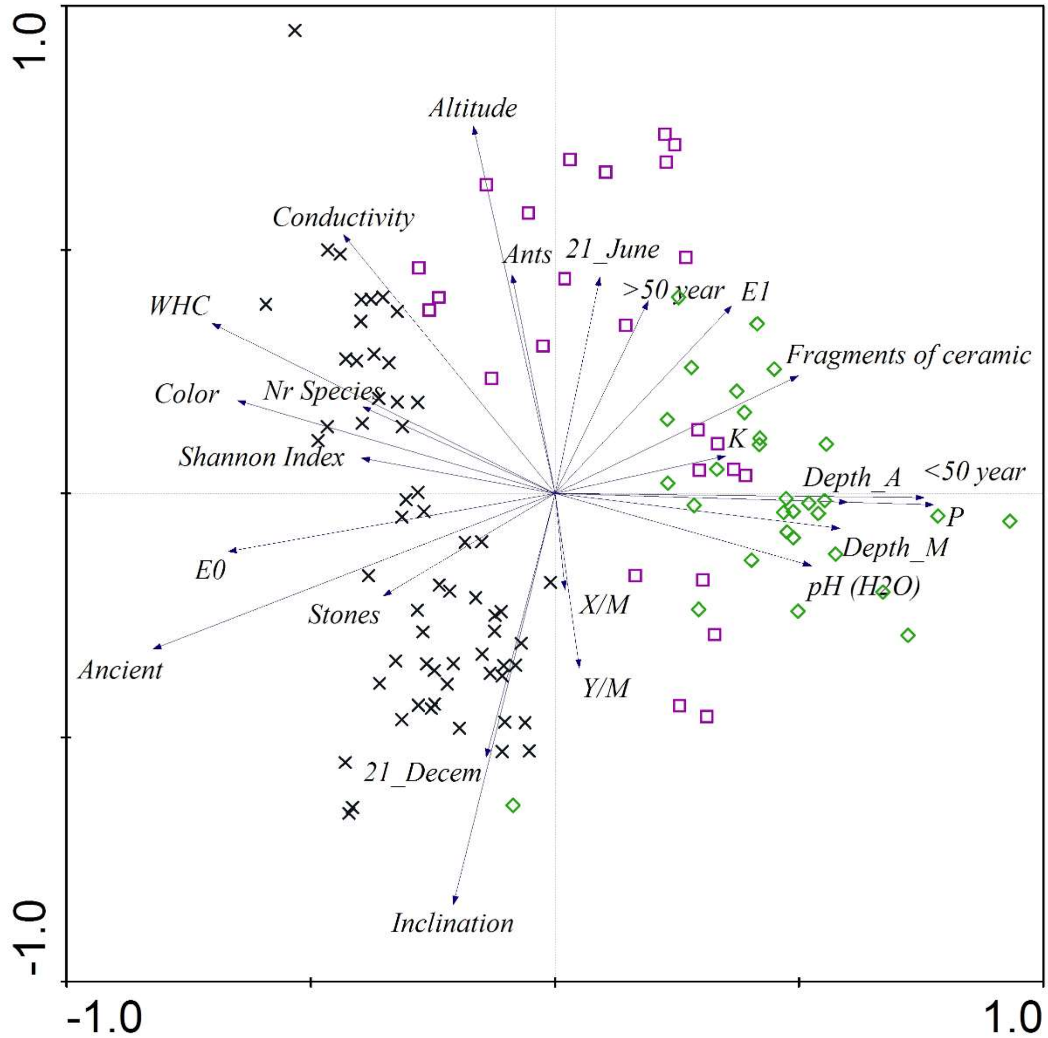

Fig. 3.4. – Principal components analysis (PCA) presenting correlations between environmental variables, namely history, altitude, slope inclination, PDSI for the two most contrasting months, soil depth (average and median), pH_{H2O}, conductivity, plant-available potassium (K) and phosphorus (P), soil colour, WHC, occurrence of anthills, number of species, Shannon–Wiener index of diversity, cover of the herb (E1) and moss (E0) layer, cover of stones, and geographic coordinates X and Y in an ordination diagram (× – ancient grasslands, □ – old recent grasslands, ◇ – young recent grasslands). Environmental variables were treated as ‘species’.

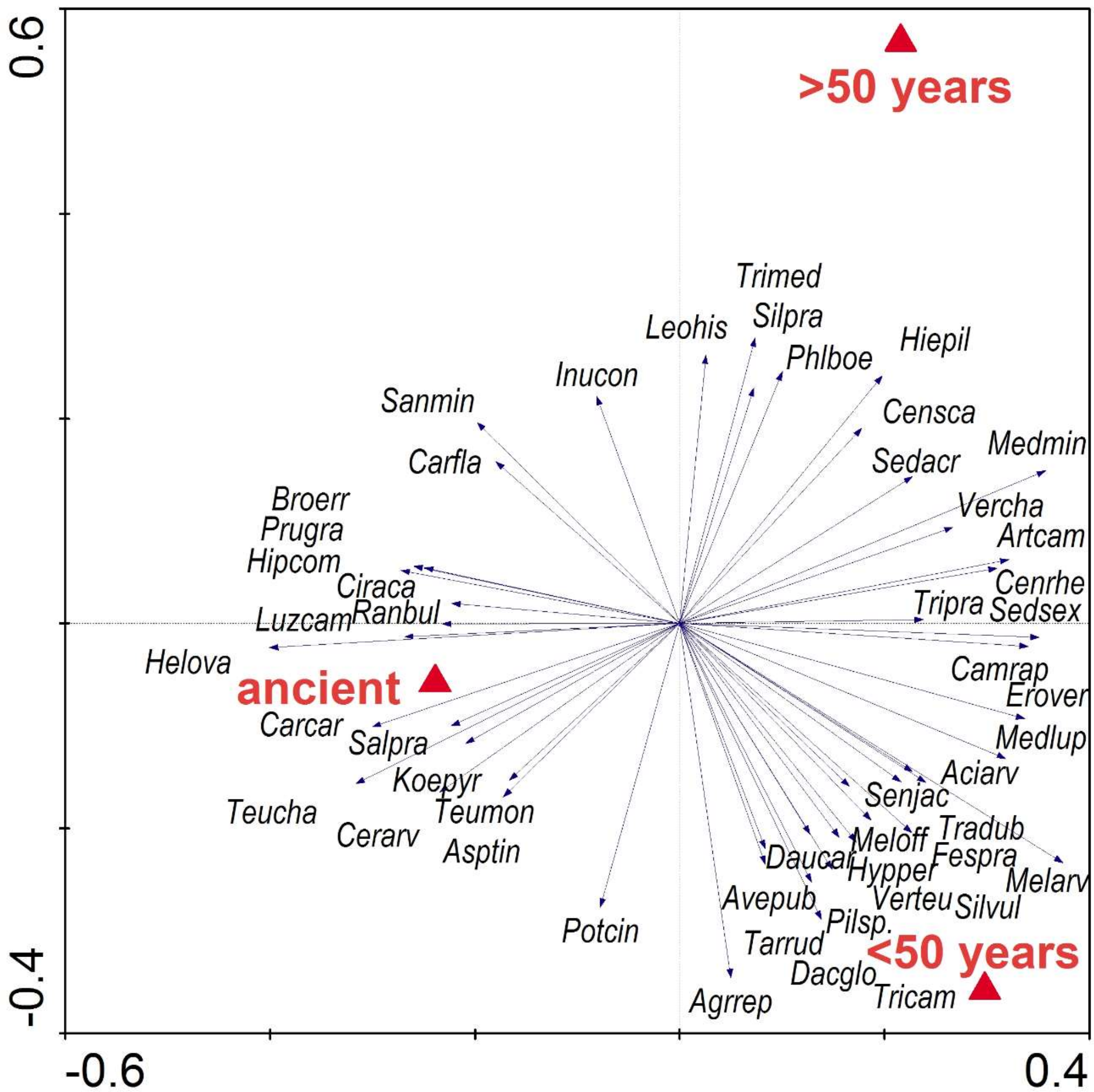

Fig. 3.5. – RDA analysis constrained by grassland history (ancient, >50 years old, <50 years old), including nine additional covariables, whose effects were subtracted. Only the 50 most correlated species (species fit range > 5%) are presented. For the full species names, see Appendix 3.1.

Table 3.4. – Results of ordination analyses (PCA, RDA) based on the dataset of 115 4-m^2 relevés. Besides variables describing the history of plots, the following environmental variables were included in the analyses: cover of the herb layer, cover of the moss layer, number of species, phosphorus content, water-holding capacity, altitude, PDSI on 21 December, and geographic coordinates X and Y. Species coverages (in percentages), with the exception of two RDAs, were transformed using the formula y = (ln x + 1) prior to the analyses.
% variance: cumulative percentage variance of species data explained by four ordination axes, % all AX: variance explained by all canonical axes together, F-statistics and significance (p-value) of Monte Carlo permutation test of significance of all canonical axes (1.999 permutations under a reduced model).

Ordination analysis	Environmental Variables	Covariables	% variance				% all AX	F-stat	p-value
			AX1	AX2	AX3	AX4			
PCA	-	-	21.7	29.1	35.6	40.4	(100)	-	-
RDA	11 (12)	0	19.6	25.4	30.2	34.0	42.7	6.980	<0.001
$RDA_{ancient\ x\ recent}$ (cover not transformed)	1	0	8.1	22.1	33.6	41.1	8.1	9.900	<0.001
$RDA_{ancient\ x\ recent}$ (cover transformed in present, absent)	1	0	14.7	22.3	29.1	33.7	14.7	19.413	0.002
$RDA_{ancient\ x\ recent}$	1	0	15.6	24.8	32.1	37.9	15.6	20.841	<0.001
$RDA_{ancient\ x\ recent}$	1	9	5.2	11.8	17.6	23.1	5.2	5.671	<0.001
$RDA_{ancient,\ old\ recent,\ young\ recent}$	3(2)	0	16.7	19.0	26.9	34.2	19.0	13.159	<0.001
$RDA_{ancient,\ old\ recent,\ young\ recent}$	3(2)	9	5.3	7.8	14.2	19.8	7.8	4.331	<0.001

Indicator species of land use history across Europe

We extracted information from 12 studies on semi-natural dry grasslands from different regions of Central and Northwest Europe and compiled a table listing the most frequent indicator species (Table 3.5). We identified a total of 120 indicator species, which we further classified into six ad hoc defined categories that took into account their exclusivity and frequency in particular datasets. In summary, 21% of them are general valid indicators of ancient grasslands (i.e. no study found them to indicate recent ones), 41% of species indicate recent grasslands (i.e. no study found them to indicate ancient ones), and 38% of identified species show contradictory results, meaning that in some studies they appear to indicate ancient grasslands whereas others found them to be indicators of recent grasslands. Many species are represented only scarcely across studies. For example, 18% of the species listed in Table 3.5 were found to have an indication ability in only two studies. The best species with a clear indication ability across different regions are *Asperula cynanchica*, *Carex caryophyllea*, *Carex flacca*, *Filipendula vulgaris*, *Helianthemum nummularium* s.l., *Hippocrepis comosa*, *Prunella grandiflora* and *Thymus praecox* s.l. for ancient grasslands and *Agrimonia eupatoria*, *Agropyron repens*, *Dactylis glomerata*, *Potentilla reptans*, *Trisetum flavescens* and *Vicia cracca* for recent grasslands.

Discussion

Characteristics of indicator species

Ancient grassland species are mostly low-growing perennials (e.g. *Carex caryophyllea*, *Potentilla neumanniana*, *Prunella grandiflora*, *Teucrium chamaedrys* and *Thymus praecox*). Indicators of recent grasslands are relatively tall, competitive plants (e.g. *Agrimonia eupatoria*, *Arrhenatherum elatius*, *Daucus carota* and *Vicia cracca* agg.) or arable weeds (*Agropyron repens*, *Melampyrum arvense*, *Myosotis stricta*, *Valerianella locusta*, *Veronica arvensis* and *Vicia hirsuta*) (Table 3.1).

Indicator species of ancient grasslands are often thought to be relicts of early Holocene vegetation. These species are not only linked to treeless grassland refuges, but also to open pine forests on stony hill tops (*Cytiso-Pinetum* and *Pyrolo-Pinetum*; Faber 1936, Gauckler 1938, cf. Pott 1995, p. 26). From such permanent pine forests (i.e. not afforested pastures) growing on rocky steep rocky slopes and rock-edges in the Jurassic mountains, Müller (1980) mentions *Hippocrepis comosa*, *Pulsatilla vulgaris*, *Teucrium chamaedrys*, *Teucrium montanum* and *Thymus praecox*, all of which are species identified as strong indicators of ancient grasslands in our study (Fig. 3.5 and Table 3.1).

Numbers of indicator species in individual grasslands

The numbers of ancient and recent indicator species in grasslands partly overlap between age categories (Fig. 3.2). This overlap was mainly caused by two older recent grasslands (nos 14 and 16). Grassland no. 14 harboured a high number of ancient grassland indicators. It is a complex of very narrow field strips on shallow soil with a low content of plant-available P and K. Between the field strips are field boundaries composed of ancient grasslands. Dispersal limitation is not strong under such conditions and ancient grassland species have optimal conditions for infiltrating into the recent grassland (Fischer 1987, Poschlod et al. 1996, Poschlod & Bonn 1998, Öster et al. 2009). Grassland no. 16 harboured a low number of recent grassland indicators. It is an area on the plateau with extremely shallow soil and a very high proportion of organic matter (WHC, $C_{organic}$), resulting in drying habitat conditions that are unfavourable for the occurrence of rather mesophilous indicator species of recent grasslands.

Environmental differences between grasslands of different age

Soil cultivation modifies soil properties. Altered soil properties may affect vegetation composition. This change is still visible over decades, centuries and even a millennium after the cessation of arable farming (Dupouey et al. 2002, Hejcman et al. 2013, Hájek et al. 2017). Ancient and older recent calcareous grasslands generally occur on shallow soil. Soil was significantly deeper only at younger recent grassland sites (Fig. 3.3), which is related to the fact that only sites with deeper soil enabled ploughing with heavy machinery, which became common since the second half of the 20th century (Poschlod 2015a). Very shallow soils were found on the plateau, which might be explained by long-term erosion and only slow weathering of horizontally oriented calcareous layers, which was also the case in another case study conducted in the Swabian Alb (Karlík & Poschlod 2009).

Soils at ancient grassland sites were more acidic (7.16 on average); the highest pH and C $_{carbonate}$ content were found in young grasslands (<50 year; 7.49 on average) (Fig. 3.3, Table 3.5). Whereas the undisturbed topsoil of ancient grasslands tends to undergo acidification over time (Helyar & Porter 1989), soils of recent grasslands have been enriched by carbonates, causing an increase of pH, due to ploughing (Coiffait-Gombault et al. 2012).

Soils in recent grasslands were richer in nutrients, evidently due to the presence of residues of fertilizers used during former arable field use. Large differences were found especially in the content of plant-available phosphorus, but potassium content was also significantly higher in recent grasslands. This pattern of soil chemistry is typical for grasslands developed on arable land and has also been noted in other studies (e.g. Römermann et al. 2005). Plant-available phosphorus plays a key role on calcareous bedrocks since phosphorus availability is very low (Marschner 2002). Phosphorus alone, or in co-limitation with plant-accessible nitrogen, is the main limiting nutrient for species richness and composition of calcareous grasslands (Janssens et al. 1998, Güsewell 2004, Hejcman et al. 2007, Fagan et al. 2008) or grassland productivity (Niinemets & Kull 2005). Persistent phosphorus deficiency is even seen as a requirement for the maintenance of high species diversity in ancient grasslands (Hájek et al 2017). Extremely low concentrations of plant-available phosphorus in ancient grasslands under study are caused by fixation of P on calcareous soils as an insoluble form of apatite (Hemwall 1957, Brady & Weil 2014). Phosphorus enrichment of older recent grasslands is the result of fertilization with dung. The highest values of phosphorus were found in younger recent grasslands, indicating the probable application of synthetic mineral fertilizers. From an agricultural perspective (VDLUFA 1997), phosphorus was a deficient nutrient in our study sites because all ancient grasslands belong to category A (very low content of phosphorus) and recent grassland belong to category B (low content) or C (optimal, achieving). Only one plot placed in an older recent grassland reached category D (high) of P content with 108 mg/kg of soil.

Potassium content was relatively high; most samples belong to category B or C (VDLUFA 1999). The increased content of potassium in recent grasslands can be partly ascribed to the application of fertilizers during arable farming in the past. The extremely high values which were measured at one young grassland locality (338 and 467 mg K/kg soil; category E according to VDLUFA 1999) were caused by input via excrements, and especially urine produced by grazing livestock, because a sheep flock was enclosed there the year before our soil sampling took place.

Other differences in soil parameters were connected with the content of organic matter. $C_{organic}$, N_{total} and WHC were significantly higher in ancient grasslands. Soil colour was darker in ancient grasslands. Ploughing during arable field use has decreased the content of organic matter by increasing the rate of decomposition. Though there are substantial differences in the amount of humus between our study sites, it seems that its quality (given by microbial decomposition activity and expressed as the C/N ratio) is similar across the study sites, as it is indicated by a non-significant difference in the C/N ratio between grassland types (Table 3.3). The rather homogeneous humus quality is probably given by the similar geological and topographical conditions of our study plots (cf. Schimel et al. 1985).

Recent grasslands are additionally distinguished by an abundant presence of various ceramic fragments, especially pieces of bricks or roof tiles (Table 3.3). Ceramic fragments were commonly disposed of as a waste on dung heaps and then spread on to fields as a fertilizer, as it is also documented for the study region (Laßleben 1998, Spörer 1999). In ancient grasslands, ceramic fragments are nearly absent, which also suggests that these grasslands were not cultivated before 1830.

Utility of indicator species in different regions

Our previous study conducted at Kaltes Feld, a region situated approximately 160 km from Kallmünz, offers the opportunity to compare indicator species that have been determined by the same method and to separate those which are of general utility and those which are limited due to specific regional conditions (Karlík & Poschlod 2009). Table 3.5 well illustrates that some species are of general validity but that the indication ability of others is restricted to only one region. Some species, typically *Salvia pratensis* (Table 3.1, Karlík & Poschlod 2009), are good indicators in both regions but indicate the opposite, which is connected with the local phytogeography of the higher-elevated Kaltes-Feld region, where hayseed with the species mentioned was probably spread on to abandoned fields (Karlík & Poschlod 2009).

If other studies are taken into account (Table 3.5), it emerges that species with a clear and high indication ability across different regions are quite scarce, examples being *Carex caryophyllea*, *Helianthemum nummularium* s.l. and *Hippocrepis comosa* for ancient grasslands and *Agrimonia eupatoria*, *Potentilla reptans* and *Vicia cracca* for recent grasslands (Table 3.5). Indicators of recent grasslands include former crops (especially fodder plants such as *Dactylis glomerata*, *Melilotus officinalis*, *Onobrychis viciifolia*, *Medicago sativa*, *Trifolium pratense* and *Vicia sativa* s.l.) and arable weeds (*Cerastium arvense*, *Cerastium holosteoides*, *Convolvulus arvensis*, *Melampyrum arvense*, *Valerianella locusta* and *Veronica arvensis* –Table 3.5). The occurrence of fodder plants is not surprising, as their cultivation on dry calcareous soils has been commonly recommended by agricultural scientists since the 19th century (e.g. Veit 1849, Stebler & Schröter 1902, Poschlod 2015a). Once more regional studies become available for evaluation, it will help to refine knowledge about the reliability of particular indicators. The inclusion of other studies can also reveal other generally valid indicators, mainly among species with phytogeographically limited distribution ranges within the reviewed regions of Central and Northwest Europe (Meusel et al. 1965–1992). Promising candidates are species with moderate or even high indication ability documented in a single study. Such species are not included in Table 3.5, which only presents species identified as indicators in two or more studies. For the indication of ancient grasslands these are: *Buphthalmum salicifolium*, *Genista sagittalis*, *Globularia bisnagarica*, *Chamaecytisus ratisbonensis*, *Pulsatilla vulgaris*, *Teucrium chamaedrys*, *Teucrium montanum* and *Verbascum lychnitis*. For recent grasslands, it is the former weed *Rhinanthus alectorolophus* or the fodder plant *Lupinus polyphyllus*.

The interregional comparison presented above uses a semi-quantitative approach. However, a more exact comparison is not possible, because these studies used different methodologies and dataset sizes, and oftentimes primary data are not published. Regional phytosociological studies are not applicable either, because they do not include information about the historical status of grasslands, nor is there usually any exact localization of plots that could be used to deduce it ex post from old maps.

Further heterogeneity between studies is caused by differences in the concept of ancient grasslands and their varied histories. Ancient grasslands in Central Europe had developed in prehistoric times (from the Neolithic onwards) or later as a result of forest grazing or clearing, and many of them have remained grasslands continuously to this day (Nelle & Schmidgall 2003, Poschlod & Baumann 2010, Robin et al. 2018). In Britain, by contrast, tillage was much more extensive before the late Middle Ages and it is supposed that most species-rich calcareous grasslands that can be considered ancient developed on former arable land (Gibson & Brown 1991, Redhead et al. 2014).

More than one third of the species listed in Table 3.5 have the opposite indication ability in different regions. We are therefore somewhat sceptical, at the present state of knowledge, that it is possible to compile a list of indicator species which could be applied across broad regions or even the whole of Europe, analogously to such lists for ancient and recent forests (Wulf & Kelm 1994).

Table 3.5. – Indication ability of grassland age (ancient or recent) across Europe. The measure of indication is mentioned at particular species: AAA very good indicator of ancient grasslands, (nearly) exclusive if number of species occurrences is large; AA good indicator of ancient grasslands; A weak indicator of ancient grasslands, exclusive if number of species occurrences is low; RRR very good indicator of recent grasslands, (nearly) exclusive if number of species occurrences is large; RR good indicator of recent grasslands; R weak indicator of recent grasslands, exclusive if number of species occurrences is low. 0 (no indication) means species present in published data set of concerned study, but without clear affinity to ancient or recent grasslands. This information may be not complete because of only limited publishing of primary data. Only species considered ancient grassland indicators in two or more studies or, analogously, species recognized as recent grassland indicators in two or more studies are presented.

Species	Karlík & Poschlod - present study	Karlík & Poschlod 2009	Forey & Dutoit 2012	Chýlová & Münzbergová 2008 (and Dipl. Thesis - Chýlová 2005)	Karlík & Malíček 2008	Ejrnæs & Bruun 1995	Ejrnæs et al 2008	Schmid et al. 2017	Cornish 1954	Fagan et al. 2008	Redhead et al. 2014	Gibson & Brown 1991	Wells et al. 1976
Localization and basic geographical description (altitude, annual mean temperature, annual mean precipitation)	south Germany, Bavaria, Kallmünz, 340-440 m, 7.8°C, 649	south Germany, Baden-Württemberg, Kaltes Feld, 650-781m, 6.5°C, 1050	central France, near Blois; 90–110 m, 12.4 °C, 635 mm	north Bohemia, Czech Republic, near Štětí, 200-310m, 9°C, 500 mm	central Bohemia, Czech Republic, Karst near Týnčany, 410-568 m, 7.5°C, 656	Denmark, north-west Zealand, Ordrup Næs, 0-120 m, 8°C, 500 mm	whole Denmark	Sweden, Baltic island of Öland, 0-57m, 7°C, 475 mm	South-east England, Kent and Surrey, North Downs, 50-170m, 11°C, 650 mm	Southern England	Southern England, Wiltshire, Salisbury Plain, 100-200 m, 10°C, 750 mm	Southern England	Southern England, Wiltshire, Porton, 100-150 m, 10°C, 769 mm
Habitat	calcareous grassland	calcareous grassland	limestone grassland	on marlstone	calcareous grassland	grasslands on well-drained soil	dry grasslands with long continuity / abandoned fields on well-drained soils	grazed grasslands on dry, neutral-to-basic sites	chalk grassland	calcareous grassland	calcareous grassland	calcareous grassland	(chalk) grassland
Nr. of samples (ancient/recent), sample area	60/55, 4m²	50/60, 4m²	3 sites (30/30), 4m²	215 patches in total (15/200)	7/5, 9m²	49 plots in total, 36m²	620/535, different areas (10m² - 1000m²)	220 plots in total, 0.16m²	34/12 sites	40 sites in 5 regions, 0.25 m² quadrats on transects	484/658, 4m² quadrats and walk-over survey	transects in 7 regions	7/10 (17 transects), 1m²
Nr. of analysed species (vascular taxa)	173	137	64	52 selected species	113	117	<600	194	51	45 presented species	144	117	100
Agrimonia eupatoria	RRR	RR		R	RRR			RRR	R		RR	RR	R
Agropyron repens	RR	R				0	RR	RRR			RR	R	
Agrostis capillaris		RR			0	0	0	A	0		AA		
Agrostis stolonifera								R	RR	RR	(R)		R
Agrostis vinealis						AA	0	A					
Achillea millefolium	R	0	0		0	0	0	0		A		RR	R
Anemone sylvestris				AAA	A								
Antennaria dioica	(A)	A			A								
Anthericum ramosum	AA			A									
Anthoxanthum odoratum		RR			R	0	0	AA		A	AA	RR	
Anthriscus sylvestris	R					0	0				RR		
Anthyllis vulneraria	AA	0	A	0	0	0	0	R	0		AA	AA	RR
Arabis hirsuta	0	R			0	AA	0	0			RR		
Arenaria serpyllifolia	A	R			0			AA			AA		RR
Arrhenatherum elatius	RRR	RR	0		0	0	0	0				RR	RR
Asperula cynanchica	AAA		0	A					AAA	AA	0	AA	A
Aster amellus		A		A									
Astragalus glycyphyllos	R	R		RRR	R								
Avenula pratensis	AA	0	0			AAA	AA	A		AA	AA	RR	A
Avenula pubescens	0	RR			0			R		AA		RR	0
Bellis perennis		R						0	RR		RR	RR	
Brachypodium pinnatum	AA	A	RR	0	0					AA	AA	AA	
Brachypodium sylvaticum								0	R			RR	
Briza media	AA	AA	A		0	AA	0	R	A	AA	0	0	0
Bromus errectus	A	0	0	0	0			0	AA	AA		RR	
Campanula rapunculoides	RR	R			RRR								
Campanula rotundifolia	A	0				0	AA	AA		AA	AA	AA	0
Carex caryophyllea	AAA	AA	AA			AAA	0	AA		AA	AA	AA	AA
Carex flacca	A	AA	A	0		AA	0	0	0	AAA	AA	0	0
Carex humilis	A										AA	AA	A
Carex muricata agg.	R							RR			AA		
Carlina vulgaris		AA		A	A			0	0		RR	AA	
Centaurea jacea	0	0	A	R		AA	AA	0					
Centaurea scabiosa	0	R		0	0	0	0	RRR			RR	A	RR
Cerastium arvense	AA	R			0			RR					RR
Cerastium holosteoides	R	RR				0	RR	0		RR		0	0
Cirsium acaule	AA	AA	A	A		AA	0	0	0	AA	0	RR	0
Convolvulus arvensis	0	R				0	0	RR			RR	R	

Cynosurus cristatus		RR				RR	0	R		RR	RR	RR	
Dactylis glomerata	RR	RR			R	0	0	RR	RR		(R)	RR	R
Danthonia decumbens	0					AA	0	AA					R
Daucus carota	RR	AA				0	0	R		R		RR	0
Euphrasia sp.	0	R							0	A	RR	RR	
Festuca ovina		0			AA	AA	AA	AA	0		AA		
Festuca pratensis	RR	RR			R	0	0	RR				R	
Festuca rubra	R	0			0			R			(R)	(R)	R
Filipendula vulgaris						AAA	0	A		AA	AA	AA	AA
Fragaria vesca		0							RR			RR	0
Fragaria viridis	R			R	0								
Galium mollugo s.l.	RR	R			0			R	0		(R)	R	RR
Galium verum	0	R	0			0	R	A		AA		AA	0
Gentianella amarella										0	0	RR	RR
Gymnadenia conopsea		A							AAA		AA		0
Helianthemum nummularium s.l.	AAA	0		0	AA			AAA	A	AA	AA	AA	AA
Hieracium pilosella	0	AA	0	0	AAA	RR	0	AA	0	RR		RR	R
Hippocrepis comosa	AA	AAA	AA						AAA		AA	AA	0
Holcus lanatus		0				0	RR		RR			RR	RR
Hypericum perforatum	0	R	0		0	0	0	0	R			RR	R
Hypochaeris radicata						0	RR	0				RR	
Knautia arvensis	RR	0	0		0	0	0	R			RR	RR	R
Koeleria macrantha	A								AA	AA	0	AA	0
Koeleria pyramidata	AA	A			0								
Lathyrus pratensis	RR	0			0			R			RR		
Leontodon autumnalis		0				RR	0	0				RR	0
Leontodon hispidus	0	A		0	0	AA	0	R	0		RR	R	0
Leucanthemum vulgare s.l.	RR	0						0	A			RR	
Linaria vulgaris	0	R										RR	R
Linum catharticum	A	A	A		0	AA	0	A	0	AA	0	RR	R
Lolium perenne		RR						RR		RR	RR	RR	
Lotus corniculatus	0	0	0	A		RR	AA	R	0	AA		RR	0
Luzula campestris	AA	RR			0	RR	0	R					
Medicago lupulina	RR	R			0	0	AA	R	R	RR		RR	0
Medicago sativa		R						RR					
Melampyrum arvense	RR	R		0	0								
Melilotus officinalis	0	R			R								
Myosotis stricta	R					R	0						
Onobrychis vicifolia		R									RR		R
Ononis repens	0	RR				0	AA				RR	RR	
Ononis spinosa		0		A				R			RR		
Orchis morio	A		0		A								
Origanum vulgare	R	0							R		AA	RR	
Pastinaca sativa									RRR			RR	R
Phleum phleoides	AA		0		0			A					0
Pimpinella saxifraga	A	0	0			0	AA		RR	AA		R	AA
Plantago lanceolata	RR	0			0	0	0	A	R			RR	0
Poa pratensis	0	RR			0						AA	RR	R
Polygala amarella		A						A					
Polygala vulgaris		0				AAA	0	R	0	A	AA	RR	AA
Potentilla neumanniana	AAA	A	0		A			A					
Potentilla reptans	RR	R				0	0	RR	R		RR	R	RR
Primulla veris	0	0				AA	0	R			AA	RR	
Prunella grandiflora	AAA		A	A				AA					
Prunella vulgaris		AA				RR			0			R	0
Ranunculus bulbosus	AA	0	0		0	0	AA	AA		A	RR	RR	0
Ranunculus repens								R	R	RR	(R)	RR	R
Rhinanthus minor	RR	0									0	R	
Rumex acetosa	R	R						R	R		AA	RR	RR
Salvia verticillata		R		R									
Sanguisorba minor	AA	0	0	A	0			0		AAA	AA	RR	0
Scabiosa columbaria	0	AA	A							AA	AA	RR	0
Senecio erucifolius		A							RRR		RR		
Senecio jacobea	R	RR				0	0	0			(R)	RR	0
Sesleria albicans	AA			0				AA					
Silene vulgaris	R								RRR			R	R
Succisa pratensis						AAA	0	A		A	AA	AA	
Taraxacum sect. *Ruderalia*	R	R				0	RR	RR		RR	(RR)	RR	R
Thymus praecox s.l.	AA			AAA						AA	AA	AA	
Thymus pulegioides subsp. *pulegioides*	0	A			0	AA	0					RR	
Trifolium campestre	RR	R	0		0						RR		R
Trifolium medium	R	0	R	0		0	0	R					
Trifolium pratense	0	RR	R			RR	0	R			RR	RR	R
Trifolium repens	0	RR				0	0	0		RR	RR	R	RR
Trisetum flavescens	R	RRR			R			RRR				R	
Valerianella locusta	R							RR					
Veronica arvensis	RR	R	0			0	0	0	R		AA	R	0
Veronica chamaerdys	RR	RRR				0	0	0			RR	R	0
Vicia cracca	RR	RR			R			RRR			RR	RR	R
Vicia hirsuta	RRR							R				A	R
Vicia sativa s.l. (incl. *angustifolia*)	RR				0	0	RR	0			RR		RR
Viola hirta	0	0	0			AA	0	0	0	AA	0	RR	0

Implications of knowledge about the historical status of grasslands for nature conservation

Before delving into a more detailed evaluation, it needs to be said that both ancient and recent grasslands in the region are very well preserved from a nature protection point of view. Of all recorded species, 36 % are valuable from a conservation standpoint (58 species in all 115 relevés; Table 3.2).

The common and easily identifiable metric used to assess the conservation value of natural or semi-natural ecosystems is species richness (e.g. Tilman & Downing 1994, Ratcliffe 2012, Capmourteres & Anand 2016). The average number of species per plot seems to be generally higher in ancient grasslands (Table 3.3), which corroborates the results of other studies (Ejrnæs & Bruun 1995, Waldhardt & Otte 2003, Fagan et al. 2008, Waesch & Becker 2009, Forey & Dutoit 2012). However, some recent grasslands are also extremely species-rich. The greatest number of vascular plant species was 46 within a 4-m^2 plot in a grassland that is 60 years old (Fig. 3.3). Analysis of the Shannon-Wiener Index of diversity leads to a similar conclusion. Significantly lower numbers of species and values of the Shannon diversity index were found in the older group of recent grasslands, which could be caused i.a. by their south-east rather than south-west orientation and associated more mesophilous conditions enabling the occurrence of somewhat more competitive species (Fig. 3.3). The total number of species in recent grasslands is even greater (84% of species on the entire species list) than that in ancient grasslands (69%) (Table 3.2). This is, however, an effect of the generally greater variability (beta diversity) of recent grasslands, which is documented i.a. by the length of the gradient in the DCA (3.46 S.D. for data for 55 recent plots versus 2.51 S.D. for 60 ancient plots, calculated without the transformation of species cover values). Thus, our results concerning species diversity are neither unambiguous nor trivial, since they contradict other studies which point out a higher value of ancient grasslands (Fagan et al. 2008, Waesch & Becker 2009, Forey & Dutoit 2012).

Other measures of conservation value concern the occurrence of red-list species or species protected by law (Table 3.2). More endangered species occur in ancient grasslands (*Anthericum ramosum*, *Chamaecytisus ratisbonensis*, *Genista sagittalis*, *Globularia bisnagarica*, *Hippocrepis comosa*, *Orchis morio*, *Prunella grandiflora* and *Pulsatilla vulgaris*), but many rare species are also typical of recent grasslands (e.g. *Melampyrum arvense*, *Petrorhagia prolifera*, *Polygala comosa* and *Silene otites*). Another example from the study region which shows a strong affinity to recent grasslands is *Gentiana cruciata* (Poschlod et al. 2008, 2009). Although less species of endangered plants occur in recent grasslands, they are a special part of the flora that does not grow in many other habitats. The high conservation value of some recent grasslands has recently been shown also by Sojneková & Chytrý (2015), who studied them in the southeastern part of the Czech Republic.

To conclude, although ancient grasslands can be considered more valuable from a nature conservancy standpoint, at least some recent grasslands are of great conservation value, too. Ancient grasslands harbour more rare and endangered species, but recent grasslands provide a habitat for endangered recent grassland specialists. Even though both types of grassland are potentially important in terms of biodiversity and harbouring of rare species, the history of grasslands is far from irrelevant. Grassland communities developed on plots of different ages can be quite unique. In addition, ancient grasslands may strongly differ from recent ones in their delivery of ecosystem services such as water retention and carbon sequestration, which are connected with higher soil organic matter content in the case of ancient grasslands (Post & Kwon 2000, Franzluebbers 2002, Lal 2004). It should also be remembered that the grasslands included in the present study, which are part of the Natura 2000 network, are extraordinarily well preserved regardless of their age. Those that are of ancient origin have not been severely degraded, and those that are recent have developed by grazing in close proximity to ancient grasslands. However, in common Central European landscapes, where farming is somewhat limited by natural constraints (also called LFAs – Less Favoured Areas), and where large tracts of arable land distant from ancient grassland sites have been abandoned and grassed over in the last decades, we can expect much greater differences between ancient and recent grasslands and the conservation value of ancient grasslands to be more pronounced.

In our opinion, distinguishing between ancient and recent grasslands will benefit nature protection. It can, for example, improve the identification and evaluation of so-called High Nature Value grasslands (Peppiette et al. 2012, Stenzel et al. 2017). Most importantly, however, grasslands of different age may also require very different management strategies if they are to be maintained. Ancient grasslands should be strictly protected against loss of area and large disturbances. On the other hand, recent grasslands may require more intense disturbances, and possibly even tillage, in order to retain particular successional stages or to regenerate the seed banks of rare weeds or low-competitive species (Kleyer et al. 2007, Schröder et al. 2008, Vymyslický et al. 2009, Karlík & Poschlod 2014).

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Appendix 3.1. – Frequency table with values of percentage constancy and median cover (using the Braun-Blanquet's scale) for each grassland site calculated from data obtained from respective five plots. The grassland numbers in the table correspond to the numbers in the map with locations of investigated grasslands in the study area (Fig. 3.1). Diagnostic species of the alliances Bromion and Arrhenatherion according to Lang & Walentowski (2010). Highly significant (P=0.001) indicator species of ancient and recent grasslands age are highlighted in bold (Table 3.1). Woody species are not presented in the table.

Grassland No.		2	5	6	7	8	9	13	15	18	20	21	23	1	4	14	16	17	3	10	11	12	19	22
Age		Ancient												Recent										
Species - Full name	Abbrev.													Old recent (>1960)					Young recent (<1960)					
Alliance *Bromion erecti*																								
Festuca rupicola	Fesrup	100 2	100 2	100 2	100 2	100 2	100 2	100 2	100 2	100 2	100 2	100 3	100 2	100 2	80 2	80 2	100 3	100 2	100 2	100 2	100 2	100 2	80 2	100 2
Brachypodium pinnatum	Brapin	100 2	100 2	100 2	100 2	60 +	100 2	100 2	100 2	100 1	100 2	100 3	100 3	100 2	40 1	100 2	.	60 1	100 1	60 2	40 1	60 1	.	80 2
Avenula pratensis	Avepra	100 2	100 1	100 1	100 1	60 +	100 +	100 1	100 1	100 1	100 2	100 2	100 2	100 3	20 2	100 2	100 2	20 2	60 1	20 2	.	40 +	60 +	100 3
Koeleria pyramidata	Koepyr	100 1	100 1	100 2	100 2	100 +	100 2	100 2	100 2	100 2	60 1	80 2	100 1	100 +	.	100 1	100 +	60 +	60 +	80 +	40 r	60 +	20 +	40 +
Carex caryophyllea	Carcar	100 2	80 +	100 1	100 2	80 +	80 1	100 1	100 1	100 2	100 2	100 1	100 1	40 +	.	60 1	.	.	.	40 1	.	.	.	.
Teucrium chamaedrys	Teucha	100 2	80 1	80 1	100 2	80 +	100 1	100 +	100 2	100 2	80 +	100 2	100 +	.	.	60 1	.	.	.	.	.	.	.	.
Phleum phleoides	Phlphl	100 1	100 +	80 1	100 2	60 +	80 +	100 1	60 2	100 2	100 +	100 +	80 +	100 1	.	100 +	100 2	100 2	40 +	40 1	.	.	.	80 1
Potentilla neumanniana	Potneu	100 +	100 1	100 2	80 +	100 +	80 +	80 +	100 2	80 +	80 +	80 +	80 +	60 +	.	80 +	100 1	.	20 r	80 +	.	.	60 +	20 1
Sanguisorba minor	Sanmin	20 +	100 +	80 1	100 r	100 +	100 1	100 +	40 +	40 +	80 +	100 +	100 +	80 +	20 r	100 +	.	40 +	.	100 +	20 r	20 +	20 +	20 r
Dianthus carthusianorum	Diacar	100 1	100 +	100 1	100 1	20 r	40 r	80 +	80 +	80 1	100 1	40 r	100 +	40 1	.	100 +	100 1	.	20 +	40 r	.	40 r	.	40 r
***Helianthemum nummularium* s.l.**	Helnum	100 1	20 +	20 2	100 1	100 1	100 1	100 2	80 2	60 +	60 1	100 2	100 2	20 1	.	60 +	.	.	.	.	.	.	.	.
Prunella grandiflora	Prugra	60 +	80 +	100 1	20 +	100 1	80 +	60 1	60 1	40 +	60 1	100 1	80 +	.	.	60 2	.	.	.	.	.	.	.	.
Asperula cynanchica	Aspcyn	100 +	60 +	100 1	100 1	40 r	80 +	60 1	100 +	20 +	80 +	.	60 r	40 +	.	80 1	.	.	.	.	.	.	.	20 r
Pimpinella saxifraga	Pimsax	100 +	100 +	100 +	60 2	100 +	100 +	40 +	20 +	40 1	60 +	20 +	40 +	100 +	20 +	100 +	.	60 +	40 1	40 r	80 +	.	.	60 +
Pulsatilla vulgaris	Pulvul	60 +	.	.	100 1	40 r	100 +	40 +	60 +	60 +	20 r	40 r	100 +	.	.	60 +	.	20 r	.	.	.	.	.	.
Medicago falcata	Medfal	40 1	80 r	100 +	40 1	.	.	.	80 +	40 +	100 +	20 +	100 +	60 +	.	40 +	40 1	20 +	20 +	.	60 1	.	40 r	60 +
Anthyllis vulneraria	Antvul	40 1	20 1	20 1	80 r	.	100 +	100 +	20 r	.	.	100 +	60 +	.	.	60 r	.	.	.	.	.	.	.	40 r
Hippocrepis comosa	Hipcom	20 r	20 +	100 +	.	40 r	40 +	40 2	40 +	20 r	.	100 +	100 +	20 1	.	20 r	.	.	.	20 +	.	.	.	.
Cirsum acaule	Ciraca	.	80 +	80 +	.	80 +	60 r	40 r	80 +	.	.	20 r	80 +	40 +	.	60 +	.	.	.	20 r	.	.	.	.
Linum catharticum	Lincat	60 +	60 +	100 +	.	.	40 r	60 1	.	.	60 +	40 r	80 +	80 +	.	60 +	.	.	20 +	40 +	20 +	20 +	.	20 +
Teucrium montanum	Teumon	40 +	20 r	60 +	80 1	20 +	60 +	40 +	60 +	.	20 +	.	80 +	.	.	.	.	.	.	.	.	.	.	.
Bromus erectus	Broerr	.	40 1	80 +	.	100 4	100 2	20 +	.	.	.	40 1	40 +	.	.	.	.	.	.	.	20 1	100 1	.	.
Scabiosa columbaria	Scacol	.	20 +	40 +	20 r	.	60 r	100 1	40 +	20 +	.	60 r	40 +	.	.	80 +	40 +	.	20 +	40 r	.	.	.	20 +
Trifolium montanum	Trimon	.	80 +	40 +	.	.	.	40 +	60 +	.	.	80 1	60 +	20 r	.	40 1	.	.	.	.	40 r	20 r	.	.
Anthericum ramosum	Antram	.	.	.	60 +	.	100 1	80 r	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Globularia bisnagarica	Globis	20 r	.	.	80 1	20 r	100 +	.	.	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea scabiosa	Censca	20 r	.	.	40 r	.	100 +	.	.	40 r	.	.	20 r	.	20 +	60 +	40 +	.	.	20 r	20 +	.	.	.
Arabis hirsuta	Arahir	.	40 +	40 r	.	.	80 +	40 r	20 +	.	.	.	.	.	.	.	.	.	.	60 +	.	20 r	.	.
Polygala chamaebuxus	Polcha	.	.	.	.	.	.	40 +	.	.	.	60 r	40 +	.	.	.	.	.	.	.	.	.	.	.
Carex humilis	Carhum	.	.	.	.	.	.	.	.	.	80 +	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys recta	Starec	.	.	.	40 r	.	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula veris	Priver	.	.	.	.	.	.	20 +	.	.	.	40 +	.	.	.	.	.	.	.	20 +	60 +	40 +	.	.
Polygala comosa	Polcom	.	.	20 r	.	.	.	.	.	.	.	20 r	.	20 r	.	20 +	.	.	.	20 +	.	20 +	.	.
Orobanche lutea	Orolut	.	.	.	20 r	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r
Erysimum crepidifolium	Erycre	.	.	.	.	20 r	.	20 2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euphorbia verrucosa	Eupver	.	.	.	.	.	.	.	.	.	.	.	40 +	.	.	20 2	.	.	.	.	.	.	.	20 1
Veronica teucryum	Verteu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 +
Other xerophilous species																								
Chamaecytisus ratisbonensis	Charat	100 1	.	20 +	100 1	100 1	40 +	40 +	100 1	100 1	60 2	60 +	100 +	20 r	.	80 1	.	.	.	20 3	.	.	.	.
Thymus praecox	Thypra	100 +	20 r	80 1	40 +	80 +	100 1	80 +	80 +	20 r	20 1	40 r	60 +	.	.	80 1	20 +	.	.	40 +	.	.	.	20 +
Potentilla cinerea	Potcin	80 r	.	.	100 1	.	20 +	20 +	100 1	80 +	.	.	80 r	.	.	40 r	20 r	.	20 +	.	.	.	.	.
Potentilla x subarenaria	Potsub	20 +	20 +	.	60 +	.	100 1	.	.	20 +	20 +	20 r	60 r	.	.	.	.	.	.	20 +	.	.	.	.
Sesleria albicans	Sesalb	.	20 +	.	20 1	.	.	100 2	.	.	.	100 2	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea rhenana	Cenrhe	20 1	40 r	40 r	40 r	.	20 +	.	.	20 +	40 r	.	.	.	.	.	40 +	40 +	.	20 +	20 +	.	.	.
Seseli annuum	Sesann	100 +	.	.	.	.	.	20 r	.	.	.	.	60 r	.	.	.	.	.	.	.	.	.	.	100 +
Taraxacum sect. *Erythrosperma*	Tarery	.	20 +	40 r	.	.	20 r	.	20 +	.	60 r	.	.	20 +	.	.	.	.	.	.	.	.	20 r	.
Peucedanum oreoselinum	Peuore	.	.	.	100 2	.	.	.	40 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Viola hirta	Viohir	.	.	.	.	40 +	.	.	.	.	.	.	60 +	.	.	20 r	.	.	.	60 +	.	.	.	20 +
Trifolium alpestre	Trialp	20 1	.	.	20 r	.	.	20 +	.	.	.	20 +	.	.	.	.	.	.	.	.	20 +	.	.	.
Thlaspi perfoliatum	Thlper	20 r	.	.	.	.	20 +	.	20 +	.	.	.	.	.	40 r	.	.	.	.	.	.	.	.	.
Koeleria macrantha	Koemac	.	60 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alyssum montanum	Alymon	.	.	.	20 +	.	.	20 +	.	20 +	.	.	.	.	.	.	.	20 +	.	.	.	.	.	.
Galium glaucum	Galgla	.	.	.	20 1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum acre	Sedacr	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	80 +	.	.	.	.	.	.	20 +
Sedum sexangulare	Sedsex	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	20 +	.	.	20 1	.	.	.	.
Acinos arvensis	Aciarv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	.	.	.	.
Medicago minima	Medmin	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	.	.	.	.	.	.	.

Alliance *Arrhenatherion elatioris*																								
Achillea millefolium	Achmil	100 1	100 1	100 1	.	100 +	100 +	100 1	100 1	80 +	20 r	100 +	100 1	100 1	100 2	100 1	100 1	100 1	100 2	100 +	100 2	60 +	100 1	100 +
Poa pratensis s.l.	Poapra	100 1	100 1	100 1	40 +	20 +	40 +	80 1	80 +	100 1	100 1	100 1	100 1	100 +	60 1	80 1	100 1	100 2	100 2	80 +	80 1	60 +	100 3	100 2
Avenula pubescens	Avepub	60 1	80 +	40 +	.	.	.	100 +	.	20 +	60 +	100 1	20 +	20 +	60 +	40 +	.	.	100 1	60 1	80 1	40 +	20 +	100 1
Medicago lupulina	Medlup	20 +	40 +	60 +	.	100 +	60 +	.	.	.	20 1	40 +	.	**100 +**	**20 +**	**100 +**	**40 r**	**20 +**	**100 +**	**100 +**	**60 r**	**80 1**	**60 1**	**100 1**
Centaurea jacea	Cenjac	.	80 +	20 1	.	.	20 r	40 r	80 +	.	.	.	60 +	20 1	.	.	.	.	.	20 1	100 1	.	.	20 1
Knautia arvensis	Knaarv	.	100 1	60 +	.	60 +	.	.	20 r	.	.	40 r	.	**100 +**	**60 +**	**80 r**	.	**20 +**	**40 +**	**100 +**	**100 1**	**80 +**	.	**60 +**
Plantago lanceolata	Plalan	.	100 1	100 1	.	.	.	20 r	.	.	20 r	.	40 r	80 +	60 +	20 +	.	.	60 1	100 +	100 +	80 1	60 +	20 +
Trifolium campestre	Tricam	.	60 r	.	.	.	.	.	.	.	60 +	.	.	.	**60 1**	.	.	.	**80 1**	**100 +**	**40 r**	**100 1**	**100 2**	.
Arrhenatherum elatius	Arrela	.	40 +	.	.	.	20 r	.	.	20 +	.	.	.	**20 +**	**100 1**	**40 +**	**20 r**	**80 +**	**100 2**	**80 1**	**100 2**	**60 +**	**100 2**	**20 +**
Tragopogon pratensis subsp. *pratensis*	Trapra	.	40 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.
Veronica chamaedrys	Vercha	.	.	.	.	.	.	.	.	20 +	20 +	.	.	**100 r**	.	**40 r**	.	.	**20 +**	**60 +**	**80 r**	.	**20 +**	**20 1**
Festuca pratensis	Fespra	.	20 +	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	60 +	60 +	20 +	40 +	.
***Vicia cracca* agg. (incl. *V. tenuifolia*)**	Viccra	.	.	20 +	.	.	.	.	.	.	.	.	.	**80 +**	**40 1**	**20 +**	.	**20 +**	**60 +**	.	**60 1**	**20 1**	**60 +**	**60 +**
Trisetum flavescens	Trifla	.	.	.	.	.	.	20 r	.	.	.	.	.	.	.	.	.	.	20 1	.	60 +	80 +	.	.
Trifolium pratense	Tripra	.	.	.	.	.	.	20 +	.	.	.	.	.	.	.	.	.	.	.	60 1	40 r	.	.	.
Tragopogon dubium	Tradub	.	.	.	.	.	.	.	.	.	20 r	.	.	20 r	.	20 +	.	.	80 +	.	20 r	20 r	.	.
Lathyrus pratensis	Latpra	.	.	.	.	.	.	.	.	.	.	20 r	.	.	100 +	.	.	20 +	80 +	.	.	.	20 r	.
Daucus carota	Daucar	.	.	.	.	.	.	.	.	.	.	20 r	.	**40 +**	.	.	.	**20 r**	**80 +**	**20 r**	**80 r**	**60 +**	**60 +**	.
Leucanthemum vulgare	Leuvul	.	.	.	.	.	.	.	.	.	.	.	20 r	20 +	20 1	.	.	.	.	80 +	20 r	80 +	.	.
Alopecurus pratensis	Alopra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 +	.	.	.
Festuca rubra	Fesrub	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 1	.	.	80 +	.
***Galium mollugo* s.l.**	Galmol	.	.	.	.	.	.	.	.	.	.	.	.	**20 r**	**20 r**	.	.	.	.	**60 1**	**60 +**	**60 1**	.	.
Cerastium holosteoides	Cerhol	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	20 r	80 +	.	.
***Vicia sativa* s.l.**	Vicsat	.	.	.	.	.	.	.	.	.	.	.	.	.	**60 +**	.	.	.	**20 +**	**40 r**	**60 r**	**100 +**	**20 1**	**40 +**
Weeds and ruderals																								
Vicia hirsuta	Vichir	.	.	.	.	.	.	.	.	.	.	.	.	**40 r**	**20 +**	**20 1**	**40 r**	**60 r**	.	.	**100 +**	**100 +**	**60 r**	**100 +**
Agrimonia eupatoria	Agreup	.	20 r	.	.	.	.	.	.	.	.	20 r	.	**100 +**	**60 1**	**40 r**	.	**40 r**	**100 1**	.	**100 1**	**80 1**	.	**40 +**
Falcaria vulgaris	Falvul	.	.	.	.	.	.	.	.	.	20 +	.	.	.	**20 1**	.	.	**20 r**	.	.	**100 r**	**20 r**	**80 +**	**80 +**
Rhinanthus minor	Rhimin	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.	.	.	.	.	100 3	100 r	.	20 2
Melampyrum arvense	Melarv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	**20 r**	**40 +**	.	.	.	**100 2**	.	.	**100 2**
Veronica arvensis	Verarv	.	.	.	.	.	.	.	.	.	.	.	.	.	**40 1**	.	.	.	.	.	**100 r**	**100 +**	.	.
Agropyron repens	Agrrep	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	.	.	.	80 +	.	20 +	.	60 +	.
Convolvulus arvensis	Conarv	.	40 r	20 +	.	.	.	.	.	.	80 +	.	.	.	20 1	20 +	40 r	.	60 +	.	.	40 r	40 +	.
Potentilla reptans	Potrep	.	.	.	.	.	.	.	.	.	.	.	.	.	**80 +**	**40 1**	.	.	**20 2**	**80 +**	.	.	.	.
Valerianella locusta	Valloc	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	.	.	.	.	20 r	.	80 r	.	.
Myosotis stricta	Myostr	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.	.	40 +	.	40 r	.	.
Melilotus officinalis	Meloff	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	60 +
Geranium cf. *columbinum*	Gercol	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	.
Cynoglossum officinale	Cynoff	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	.
Silene latifolia subsp. *alba*	Silpra	.	.	.	.	.	.	.	.	.	.	.	.	40 r	.	.	.	.	.	.	.	.	.	.
Other species																								
Galium verum	Galver	100 2	100 2	100 2	100 2	100 1	60 +	100 2	100 2	100 1	100 1	100 2	100 2	100 1	100 1	100 1	100 2	100 1	100 1	100 1	80 +	80 1	100 2	100 1
Euphorbia cyparissias	Eupcyp	**100 +**	**100 +**	**100 +**	**100 1**	**60 +**	**100 1**	**100 2**	**100 1**	**100 +**	**80 +**	**100 2**	**100 1**	80 1	40 r	80 1	100 +	80 1	40 +	20 1	40 +	60 +	40 +	100 1
Securigera varia	Secvar	80 1	100 2	80 +	60 1	80 +	20 +	80 r	60 1	100 +	60 +	.	60 +	100 1	100 +	80 1	100 1	100 1	100 2	100 +	80 +	80 +	60 +	100 1
Plantago media	Plamed	80 r	100 +	80 +	20 +	80 r	.	80 +	80 r	.	80 +	80 +	100 +	100 1	20 +	100 1	.	.	60 +	80 2	100 1	100 1	40 2	80 +
Fragaria viridis	Fravir	.	100 2	100 2	20 1	60 +	.	.	40 2	60 2	100 2	.	.	100 1	100 2	80 +	.	40 2	100 2	60 2	60 1	80 +	80 1	40 +
Salvia pratensis	Salpra	**100 2**	**60 2**	**20 +**	**100 2**	**100 2**	**100 2**	**60 +**	**80 +**	**100 1**	**80 1**	**60 1**	**100 +**	.	.	20 1	.	.	.	80 1	.	.	40 +	40 r
Briza media	Brimed	**100 +**	**60 +**	**40 1**	**80 +**	**100 1**	**80 +**	**80 1**	**100 +**	.	**20 +**	**100 1**	**100 +**	100 +	.	60 1	.	.	.	80 1	60 r	20 1	.	.
Taraxacum sect. *Ruderalia*	Tarrud	20 r	100 +	100 +	.	.	.	.	20 r	.	60 r	.	100 +	100 +	60 +	20 1	.	20 r	100 2	40 r	40 r	100 1	100 +	60 r
Ranunculus bulbosus	Ranbul	**20 +**	**100 1**	**100 2**	**20 r**	**100 r**	.	**80 r**	**20 +**	.	**100 +**	**60 +**	**100 +**	60 r	.	80 r	.	.	40 r	20 +	.	40 +	60 +	.
Lotus corniculatus	Lotcor	20 r	.	40 +	60 r	20 +	40 +	40 +	20 r	.	100 +	40 r	100 +	100 +	.	80 +	.	.	40 +	60 +	40 1	80 1	.	100 +
Cerastium arvense	Cerarv	.	**100 1**	**80 +**	**80 +**	**40 +**	.	**100 1**	**80 1**	**20 1**	**80 r**	.	**60 +**	20 +	.	40 r	.	.	.	20 +	.	.	20 +	20 1
Dactylis glomerata	Dacglo	.	60 +	20 +	.	40 r	.	20 +	40 +	.	.	20 r	.	**40 +**	**40 +**	.	.	**20 +**	**100 1**	**80 +**	**60 1**	**40 r**	**80 +**	**40 r**
Hieracium pilosella	Hiepil	.	40 +	80 +	20 1	20 +	80 r	.	.	.	20 +	.	60 r	60 +	.	40 +	40 r	80 +	.	40 r	.	.	.	40 +
Hypericum perforatum	Hypper	.	60 r	20 +	.	20 r	.	.	60 +	40 +	.	.	.	60 r	20 r	40 r	.	40 +	80 r	40 r	20 r	.	.	40 r
Campanula rotundifolia	Camrot	.	20 +	20 +	.	60 r	.	80 +	40 +	20 r	.	20 +	80 +	20 r	.	.	.	.	.	40 r	60 r	.	.	.
Luzula campestris	Luzcam	**20 +**	**100 +**	**20 r**	.	.	.	**40 r**	**40 +**	.	**100 +**	**100 +**	**20 +**	.	.	.	.	.	.	.	.	.	.	.
Arenaria serpyllifolia	Areser	.	.	20 +	20 1	.	100 +	.	60 r	80 r	20 r	.	.	.	.	.	40 +	20 +	.	20 +	.	.	.	.
Senecio jacobaea	Senjac	.	20 +	.	.	.	.	20 r	20 r	.	20 +	.	.	40 r	.	20 r	.	.	40 +	40 r	.	40 r	.	80 r
Cerastium pumilum agg.	Cerpum	.	.	.	.	.	40 r	.	.	.	.	.	.	.	60 1	.	40 r	.	.	60 +	.	100 +	.	.
Genista sagittalis	Gensag	**20 +**	.	.	**20 2**	.	.	**60 +**	**20 1**	.	.	**100 1**	**40 +**	.	.	.	.	.	.	.	.	.	.	.
Thymus pulegioides	Thypul	.	60 +	.	.	.	.	20 +	.	.	60 1	20 +	.	40 +	.	20 +	.	.	.	20 +	.	.	.	.
Carex flacca	Carfla	.	.	.	.	20 2	.	20 1	20 1	.	.	40 +	100 1	.	.	40 +	.	.	.	.	.	.	.	.
Campanula rapunculoides	Camrap	.	.	.	.	.	.	.	.	.	.	.	.	**20 +**	.	**40 +**	**20 +**	.	**40 r**	.	**40 r**	.	**40 +**	.
Orchis morio	Orcmor	.	20 r	100 +	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Artemisia campestris	Artcam	.	.	.	.	.	.	.	.	.	20 +	.	.	.	.	.	20 2	40 +	20 +	.	.	.	.	20 1
Anthriscus sylvestris	Antsyl	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	80 r	40 +	.	.
Ajuga genevensis	Ajugen	.	40 r	20 r	.	.	.	.	.	40 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium pumilum	Galpum	.	.	.	.	.	.	40 r	.	.	.	.	60 r	.	.	.	.	.	.	.	.	.	.	.
Leontodon hispidus	Leohis	.	.	.	.	.	.	.	.	.	.	20 +	20 r	60 2	.	.	.	.	.	.	.	.	.	.
Silene vulgaris	Silvul	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	20 1	.	.	.	.	60 r

Astragalus glyciphyllos	Astgly	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 1	60 +	.
Trifolium medium	Trimed	.	.	.	.	.	.	.	.	.	.	.	.	80 r	.	.	.	.	.	.	.	.	.	.
Euphrasia sp.	Euphra	.	.	40 +	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.	.	.	.	.	.
Echium vulgare	Echvul	.	.	.	.	.	40 r	.	.	.	.	.	.	.	.	.	.	.	.	20 1	.	.	.	.
Inula conyza	Inucon	.	.	.	.	.	.	20 +	.	.	.	.	.	.	.	.	.	40 r	.	.	.	.	.	.
Carex muricata agg.	Carmur	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.	.	.	20 1	.	.	.	20 1
Erophila verna	Erover	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	60 +	.	.	.	.
Platanthera sp.	Plasp.	.	.	.	.	20 r	20 r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sedum maximum	Sedmax	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	.	.	.	.	.	.	.	20 +
Allium oleraceum	Allole	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 +	.	.	.	.	.	.	20 r	.
Arabis glabra	Aragla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 +	.	.	.	.	.	.
Pilosella sp.	Pilsp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 +	.	.	.	.	.
Trifolium repens	Trirep	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20 r	.	20 r	.	.
Origanum vulgare	Orivul	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40 r	.	.

Species in only one plot

Artemisia vulgaris 3, *Asperula tinctoria* 15, *Campanula patula* 4, *Carlina acaulis* 6, *Cuscuta epithymum* 23, *Danthonia decumbens* 6, *Galium pomeranicum* 4, *Linaria vulgaris* 17, *Muscari comosum* 1, *Ononis repens* 1, *Petrorhagia prolifera* 16, *Phleum pratense* 19, *Plantago major* 4, *Poa compressa* 9, *Polygonum aviculare* 11, *Rumex acetosa* s.l. 19, *Silene otites* 3, *Stellaria graminea* 10, *Trifolium dubium* 10, *Vicia tetrasperma* 19, *Vincetoxicum hirundinaria* 15, *Viola arvensis* 4.

Chapter 4
Soil seed bank composition reveals the land-use history of calcareous grasslands

Abstract:
We compared soil seed banks and vegetation of recent (established on abandoned arable fields) and ancient (continuously managed as pastures at least since 1830) calcareous grasslands if there is any impact of former arable field use. The study was carried out in two regions of Southern Germany with well-preserved dry grassland vegetation: the western Jurassic mountains (Kaltes Feld) and the climatically drier eastern part of Southern Germany (Kallmünz).

Total number of species in the seed bank was similar in both regions, but species composition partly differed, reflecting phytogeographical differences between the regions. The total number of emerged seedlings showed a large disparity (5457 compared to 2523 seedlings/m^2 in Kaltes Feld and Kallmünz, respectively).

Though there were differences in seed bank composition and size, we found a uniform pattern of plant traits (affiliation to phytosociological groups, Raunkiaer plant life-forms and seed longevity), which depended on the age of the grassland.

The main conclusion is that seed banks in contemporary calcareous grasslands still reflect the history of former land use – in this case arable cultivation, even though it occurred a long time ago (up to 150 years). Indicators of former arable fields are germinable seeds of weeds which have persisted in the soil to the present. By contrast, weedy species are completely absent from the seed banks of ancient grasslands. Soil seed banks of recent grasslands may be of substantial conservation importance because they may store seeds of rare and endangered weed species such as *Kickxia spuria*, *Silene noctiflora* and *Stachys annua*, the majority of which have already gone extinct from the current vegetation of the study sites.

Keywords: Ancient grasslands; Calcareous grasslands; Jura; Rare weeds; Recent grasslands; Similarity index

Introduction

Semi-dry calcareous grasslands are among the oldest man-made habitats in central Europe and belong there to the most species-rich habitats (Dutoit et al., 2009; Poschlod et al., 2009; Poschlod and Baumann, 2010). Many sites have existed continuously, while numerous others have undergone a varying degree of land-use changes (e.g. Mailänder, 2005). Large areas of calcareous grasslands were transformed into arable fields during the human population increase after the Thirty Years' War (Ehmer, 2004; Pfister, 2007; Poschlod 2015a). The strong decrease in the area of calcareous grasslands was accelerated after the mid-19th century when the sheep population in Germany dropped drastically because of imports of cheap wool from Australia and New Zealand (Poschlod and WallisDeVries, 2002). On the other hand, intensification of agriculture, especially after the Second

World War, caused fields with less favourable conditions for arable land use to be turned into recent grasslands (Baumann et al., 2005; Mailänder, 2005).

There are different approaches to studying the land-use history of grasslands (Poschlod et al., 2009). Researchers have either applied different palaeoecological methods (Poschlod and Baumann 2010) or analysed soil seed banks, as we have done in the present study. Seeds of certain species, especially arable weeds, are well known to remain germinable for long periods, even for 100 years or longer (Priestley, 1986; Telewski and Zeevaart, 2002).

Studies of old fields and grassland succession often reflect the influence of time on the soil seed bank, but only a few papers, such as Forey and Dutoit (2012), have compared grasslands which have been continuously managed as grasslands (at least since the Middle Ages, if not since the Roman or Bronze Age) with recent grasslands established on former arable fields (since the beginning of the 19th century). Today, these two categories of grasslands are subject to similar ecological conditions.

Soil seed banks of grasslands have been frequently studied since the 1950s (Bogdanovskaya-Gienef, 1954; Rabotnov, 1956; 1969) and especially since the 1970s (e.g. Míka, 1978; Thompson and Grime, 1979). Seed banks of dry calcareous grasslands of different age were studied in the second half of the 1970s in the Czech Republic (Soukupová, 1984; Soukupová, 1990), in the 1980s and 1990s in Germany (Poschlod et al., 1991; Poschlod, 1993a; Poschlod and Jackel, 1993; Poschlod et al., 1998) and England (Hutchings and Booth, 1996), and recently also in France (Römermann et al., 2005, Buisson et al., 2006, Forey and Dutoit, 2012). Dutoit and Alard (1995) demonstrated the effect of various management regimes on the soil seed bank of limestone grasslands in northern France. Fischer (1987) was one of the first who found germinable weed seeds in the soil seed bank of dry grasslands and who interpreted them as possible indicators of former arable field cultivation.

Succession of abandoned arable fields towards grasslands may proceed very quickly. Since seed production of arable weeds and early fallow species is relatively high, early successional grassland stages may contain high amounts of seeds in the seed-bank. During the time the role of generative reproduction decreases (Soukupová, 1984; 1990). Vegetation of recent grasslands may have reached a nearly stable state thirty to fifty years after field abandonment consisting already of late fallow and grassland species (Ruprecht, 2005; Jírová et al., 2011).

Dry calcareous grasslands maintain high species diversity including numerous rare plant taxa (e.g. Korneck et al., 1998; Wallis DeVries et al., 2002; Dengler, 2005). They therefore represent habitats of high conservation value. Studies concerning grasslands and especially dry calcareous ones show that restoration of former diversity from the soil seed bank after disappearance of species from the aboveground vegetation is strongly limited (e.g. Graham and Hutchings, 1988; Willems, 1995; 2001; Bakker et al., 1996; Bekker et al., 1997; Poschlod et al., 1998; Mitlacher et al., 2002; Bossuyt and Hermy, 2003; Bisteau and Mahy, 2005; Valkó et al., 2011). Arable weed communities on former less intensively exploited arable fields on shallow calcareous soils have today also a high conservation value. Many formerly widespread weed species are now regionally extinct and maintain only few populations in the Jurassic mountains (e.g. Breunig and Demuth, 1999; Scheuerer and Ahlmer, 2003). In contrast to grassland species arable weeds are known to have a long-term persistent seed bank (Priestley, 1986; Bekker et al., 1998a; b).

We therefore address the following questions:

1) How does the composition of the soil seed bank of ancient grasslands compare to recent grasslands of different age?

2) How similar is the soil seed bank to aboveground vegetation? Is there a greater similarity among ancient grasslands?

3) Does the soil seed bank of recent grasslands reflect any information about former arable field use of these sites?

4) What is the general effect of former cultivation and age of grasslands on soil seed bank composition when species are divided into groups according to their ecology and when selected plant traits are analysed?

5) Is the soil seed bank valuable for the conservation of rare arable weeds?

We compare the contemporary features of grasslands of different ages. In addition, we derive some interpretations from space-for-time substitution results, an approach commonly used in current research on succession (Öster et al., 2009, Csecserits et al., 2011, Johansson et al. 2011, Török et al., 2011).

Various factors influence the composition of the soil seed bank; the climate plays an important role, for example. We therefore collected data from two calcareous grassland regions of the Jurassic mountains in southern Germany, which differ in their climate – one is more suboceanic and the other more subcontinental – but which are comparable as to their geology and vegetation.

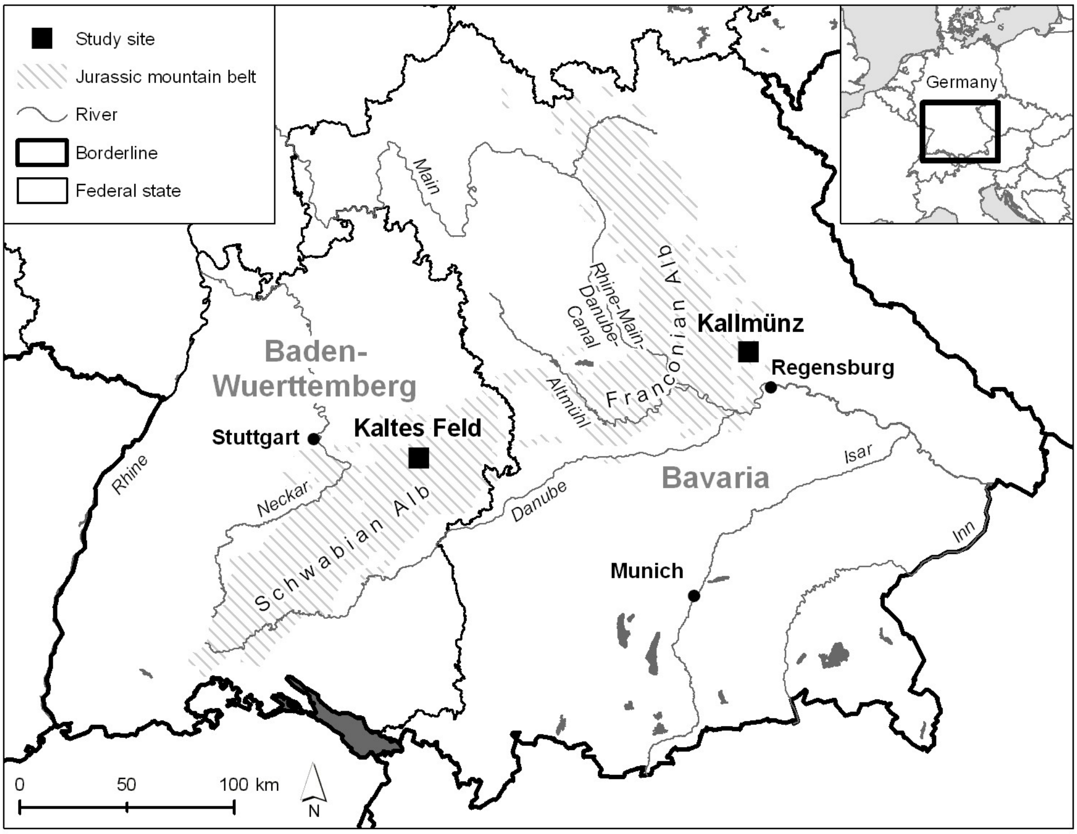

Fig. 4.1. – Locations of study areas.

Methods

<u>Study regions</u>

The two study regions are situated in the German part of the Jurassic mountains. Kallmünz is located in the Franconian Alb (Bavaria) and the Kaltes Feld in the Swabian Alb (Baden-Württemberg; Fig. 4.1).

Kallmünz is a small town ca. 20 km northeast of Regensburg at the confluence of the rivers Naab and Vils. Elevations range from 340 to 440 m above sea level, and mean annual precipitation is 649 mm. Kaltes Feld is located 50 km east of Stuttgart and approximately 160 km from Kallmünz. The altitude ranges from 650 to 781 m above sea level, and mean annual precipitation is 1050 mm.

The climate of both regions is temperate – subcontinental near Kallmünz and subatlantic at Kaltes Feld.

The bedrock of both study areas belongs to the Malm series, an upper Jurassic formation consisting mainly of solid or hard reef limestone. At Kaltes Feld, marlstone may also occur (Müller, 1961; Meyer and Schmidt-Kaler, 1995; LGRB Ba-Wü, 2002; Geyer and Gwinner, 2008).

The main soil type in both regions is Rendzina, partly developed as brown soil. Soils are mainly very shallow.

Because of the large extent and high conservation value of the dry grasslands, both areas are included in the European Natura 2000 network under the Habitats Directive 92/43/EEC (site code and site name: 6838–301 Dry slopes at Kallmünz and 7224–342 Albtrauf Donzdorf-Heubach).

Due to the high diversity and the occurrence of rare and relict species, the study of calcareous grasslands in the South German Jurassic mountains has a long tradition (Gradmann, 1898; 1950; Gauckler, 1938). The dry grassland vegetation near Kallmünz has been described by Sendtko (1993) and at Kaltes Feld by Jandl (1988). Grasslands of both study regions belong to the association *Gentiano-Koelerietum* (alliance *Mesobromion*) and various initial or degraded stages of this association. At Kallmünz, the association *Pulsatillo-Caricetum humilis* (alliance *Xerobromion*) (Sendtko, 1993) is also characteristic. However, this *Xerobromion* community was not considered and sampled here.

The flora of both regions is similar but differs in the proportion of certain phytogeographical elements. Near Kallmünz, there are more xerothermic species and species with more continental distribution (*Chamaecytisus ratisbonensis* – western border of distribution area, *Artemisia campestris, Potentilla cinerea, Seseli annuum, Silene otites*). At Kaltes Feld, true xerothermous species are rare, but certain dealpine species like *Buphthalmum salicifolium, Gentiana verna* and *Stachys alpina* are quite common.

Calcareous grasslands of both study areas are being used as pastures. There is no indication of hay-making in neither region, but we can assume people made hay at least at Kaltes Feld in the more distant past. Besides cattle and other domestic livestock, sheep grazing was hugely important, especially practised as the so-called South German transhumance (Hornberger, 1959; Poschlod and WallisDeVries, 2002).

A significant part of the current calcareous grasslands had once been used as arable fields, but were converted into grasslands in different times for different reasons (new farming methods, socio-economic changes). Land use history was studied in detail at Kaltes Feld by Mailänder (2005) and at Kallmünz by Baumann et al. (2005). The effect of land use history on vegetation composition has been shown, for example, by Poschlod et al. (2008) and Karlík and Poschlod (2009).

Grasslands analysed in this study were selected using cadastre maps from 1830 onwards. As ancient we consider grasslands which have been continuously managed as pastures at least since 1830 – often, however, since the Roman period or even Neolithic Age (Baumann, 2006; Poschlod and Baumann, 2010). As recent we consider grasslands marked as arable land at least in the first cadastre map from 1830. We ascertained the age of the recent grasslands using maps surveyed after 1830, aerial photographs from 1945 and by interviewing the oldest residents.

Table 4.1. – Location, geographical characteristics and age of the grasslands under study (K – Kallmünz, F – Kaltes Feld).

Locality code	**Approx. age in the year 2007 (**time since conversion to grassland)	**Position – longitude** (WGS84)	**Position – latitude** (WGS84)	**Altitude and slope** (mean with boundary values)
Kallmünz				
K180a	ancient (>180)	11º57'22"	49º09'00"	365 m, 14º SW (11–15)
K180b	ancient (>180)	11º58'39"	49º09'59"	385 m, 11º S (3–15)
K90	90	11º58'27"	49º09'44"	380 m, 16º S (10–20)
K60	60	11º57'36"	49º09'03"	412 m, 1º SW (0–3)
K40	40	11º56'34"	49º09'59"	370 m, 14º W (10–20)
K15a	15	11º59'38"	49º10'13"	370 m, 3º S (1–4)
K15b	15	11º58'50"	49º09'32"	365 m, 15º S (14–15)
K0	arable field (0)	11º59'25"	49º10'15"	370 m, 5º S
Kaltes Feld				
F180a	ancient (>180)	9º53'34"	48º43'38"	654 m, 25º S (23–27)
F180b	ancient (>180)	9º52'46"	48º44'20"	684 m, 10º W (8–12)
F153	153	9º50'54"	48º44'05"	776 m, 3º W (2–4)
F100	100 (>>55)	9º50'34"	48º43'49"	694 m, 8º SW (2–12)
F50a	50	9º51'12"	48º43'21"	590 m, 18º S (17–20)
F50b	50	9º53'02"	48º43'46"	656 m, 13º S (11–15)
F8	8	9º50'59"	48º43'41"	765 m, 2º SW (0–5)
F0	arable field (0)	9º50'50"	48º44'02"	772 m, 3º W (3–4)

Soil seed bank and vegetation composition

In both regions, we selected eight grassland localities. Each of these sets comprised localities of different age: ancient grasslands, fallow fields converted into grasslands long time ago, localities converted into grasslands 50–60 years ago, very young grasslands and currently cultivated arable fields (Table 4.1). The selected grasslands were mainly surrounded by other grasslands, hedges or woodlands and in few cases also by arable fields. In this case, the grasslands were chosen with the intention to minimize possible effects of fields (especially seed rain) although seeds of arable weeds have strongly limited dispersal potential (Bonn and Poschlod, 1998). Within each grassland, we randomly selected five 2×2 m plots, however, excluding rocks or shrublands (for details see Poschlod et al., 2008; Karlík and Poschlod, 2009). For every plot, we recorded the actual vegetation by applying the Braun-Blanquet's (1964) nine-grade abundance-dominance scale. Furthermore, we collected data on different environmental variables such as the slope and aspect, grassland biodiversity measures expressed by species number in aboveground vegetation and the Shannon-Wiener index for every plot. We used data on latitude, slope and aspect to calculate potential direct solar radiation. The calculation was done on the 21st day of each month between December and June following Jeník and Rejmánek (1969).

We took seed bank samples in March 2007 following the recommendations of Bakker et al. (1996). Sampling in early spring ensures seed stratification during the winter, yielding more accurate information about the soil seed bank. We opted for the emergence method and did not look for ungerminated living seeds remaining in the soil after the emergence experiment because the floating, separation and testing for viability is enormously labour-intensive and because determination on the species level is often impossible (ter Heerdt et al. 1996). In each plot, we took ten randomly chosen samples using a soil corer with a diameter of 40 mm. Each core was taken to the depth of 10 cm because a many grasslands have shallow soil, so sample taking from deeper layers is infeasible. We removed litter and mosses to eliminate the occurrence of recent seeds (Fischer, 1987). Then we divided each core into two sections: from 0–5 and 5–10 cm depth. For each plot, we pooled together 10 of these corresponding sections. This produced a total sample area of 126 cm^2 (1.26 litre) for each vegetation plot, or 628 cm^2 (6.28 litre) for each grassland or arable field. The sample volume of more than six litres per locality corresponds to the volume recommended by the literature (e.g. Hutchings, 1986). In total, we sampled 40 vegetation plots (nearly 50 litres of soil) at each of the two regions.

The soil samples were transported in plastic bags to the laboratory and stored at 4°C until processing. In order to reduce the sample volume and establish better germinating conditions, the sampled soil was washed through a two-stage sieve cascade of 5 mm (to remove stones and roots) and 0.2 mm (to remove fine-soil without seeds) according to the recommendations of ter Heerdt et al. (1996). The soil samples were then spread in thin layers of approximately 3 mm into trays on a layer of approximately 4 cm horticultural substrate, which was sterilized under hot steam (N=80 per region). To check for any contamination of the samples by the underlying substrate or by wind-borne seeds during the cultivation, additional trays with only sterilized substrate were randomly distributed within each sample set per locality. Seedlings of *Betula* sp., *Salix* spp., *Epilobium* spp., *Taraxacum* sect. *Ruderalia,* etc. established in these trays and were therefore not taken into account for further analyses.

Samples in the trays were cultivated in a nonheated greenhouse, allowing natural temperature fluctuations during day and night but prohibiting any disturbance or predation by animals such as birds or mice. Samples were carefully watered to ensure that no seeds would be washed away. Cultivation lasted from the end of March 2007 until May 2008 when nearly no new seedlings appeared any more. Seedlings were removed in the seedling stage. If identification was not possible in this stage, they were planted in separate pots and grown until they could be identified. In a few cases, taxonomically difficult species or those which could not be separated were merged, for example, *Leucanthemum vulgare* agg. or *Chenopodium album* agg. (among exactly determined *Chenopodium* species, *Chenopodium album* s. str. was dominant; however, also *C. pedunculare* and *C. ficifolium* were found in the seed bank at Kallmünz). The number of unidentifiable seedlings (mainly because they died before they could be identified) amounted to less than 0.5% of the total number of seedlings.

Taxonomic nomenclature follows Rothmaler (2005).

<u>*Data analysis*</u>

For each plot, we counted the number of species in both the vegetation and the seed bank and the number of seedlings that emerged from the soil samples. In order to reduce the amount of results presented below, we pooled the data from the two soil depths in further analyses (N=40 per region). To obtain data for whole localities (N=8 per region), we summed up the data from individual plots.

We used Sørensen's similarity index to analyse the floristic similarity between aboveground vegetation and the seed bank. There are more similarity indices and their modifications, but Sørensen's index is the one used most often, which enables comparisons with the largest number of studies (Hopfensperger, 2007). We calculated the similarity index for each plot (N=40) and for each locality (N=8) using the formula: Sørensen´s similarity index = 2C/(A+B), where "C" is number of species common to the vegetation and the seed bank, "A" is the total number of species in the vegetation, and "B" is the total number of species in the seed bank.

Calculation of similarity indices was done using EXCEL (Microsoft, 2000). Univariate statistical analyses were run in STATISTICA 8.0 (StatSoft, 2007), and multivariate analyses were done in CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002). To evaluate species composition of the seed bank using multivariate analyses, we employed unimodal ordination methods (detrended correspondence analysis – DCA and canonical correspondence analysis – CCA; ter Braak and Šmilauer, 2002). This was warranted by the large length of the gradient of the first axis (more than 4 S.D. units), which was 7.7 in Kallmünz and 6.0 in Kaltes Feld. Since the results of ordinations with and without transformation of species frequency in plots were similar, only results without species transformation are presented. We carried out a one-way ANOVA with a subsequent post-hoc test (modification of the Tukey HSD test for unequal N) to assess the relationships among seed bank density, the number of species in the seed bank, plot similarity (vegetation × seed bank) and the age of the grassland.

Traits of plant species

To generalize and, as far as possible, clarify the effect of land use history on soil seed bank composition, we analysed plant traits of seed bank species occurring in grasslands of different age. First, we sorted species into groups according to their ecology, which were related to phytosociological groups (using reference books of Chytrý, 2007 and Rothmaler, 2005), namely xerophilous species from the classes *Festuco-Brometea* and *Sedo-Scleranthetea* (first group), mesophilous grassland species from *Molinio-Arrhenatheretea* (second group) and weedy or ruderal species from *Stellarietea mediae* and *Artemisietea vulgaris* (third group). Grassland species with a broad ecological range such as *Centaurea jacea* and *Pimpinella saxifraga* or species from other vegetation units such as *Clinopodium vulgare* were put in a fourth group called "other species".

Secondly, we categorized species by their life form according to Raunkiaer: therophytes, geophytes, hemicryptophytes and chamaephytes. We assigned life forms to particular species using Ellenberg et al. (1992) and Kubát et al. (2002).

We extracted seed mass averages for every species from the BioPop and LEDA Traitbase (Poschlod et al., 2003, Knevel et al., 2003; Kleyer et al., 2008; http://www.leda-traitbase.org). We determined the longevity of each species (transient, short-term persistent, long-term persistent) and calculated its longevity index using criteria and data of Thompson et al. (1997; 1998). Although the longevity index sensu Thompson was recently criticized by Saatkamp et al. (2009), there is still no better generally usable measure of seed bank persistence.

We obtained data on seed length, width and height from BioPop (Poschlod et al., 2003; Jackel et al., 2006). Because many species have detachable appendages on seeds or fruits, we prepared two datasets: one with and one without them. From absolute seed length, width and height, we calculated relative values (when seed length equals 1) and then computed the seed shape using the formula given in Bakker et al. (1996).

Results

Seed bank in the Kallmünz region

The seed bank composition in the Kallmünz region is shown in Table 4.2 and in Appendix 4.1. The most frequent species present in the seed bank of nearly every plot were (i.e. without regard for the quantity in particular plots; sorted in descending order) *Poa angustifolia, Hypericum perforatum, Anagallis arvensis, Carex caryophyllea, Potentilla neumanniana, Chenopodium album* agg., *Medicago lupulina* and *Daucus carota*. We found high numbers of seedling individuals of *Digitaria ischaemum, Hypericum perforatum, Poa angustifolia, Chaenorhinum minus, Daucus carota, Carex caryophyllea, Potentilla neumanniana* and *Anagallis arvensis*.

Typical dry grassland species were not very frequent in the soil seed bank. The only frequent species were *Carex caryophyllea* and *Potentilla neumanniana*. Some dry grassland species such as *Dianthus carthusianorum, Chamaecytisus ratisbonensis, Anthyllis vulneraria* and *Globularia bisnagarica* were detected only sporadically in the soil seed bank of ancient grassland samples (K180b). In recent grasslands, by contrast, several arable weed species such as *Anagallis arvensis, Chenopodium album, Digitaria ischaemum* and *Chaenorhinum minus* were relatively frequent in the soil seed bank. Even endangered or locally rare species were represented, namely *Neslia paniculata*

(K15b), *Silene noctiflora* (K15b) and *Phleum nodosum* (K15b). In addition, some typical fallow field species were frequently found in the soil seed bank, for example, *Hypericum perforatum* and *Daucus carota*.

Table 4.2. – Composition of the seed bank of Kallmünz and Kaltes Feld. Numbers of seedlings in samples of all analysed localities are shown (total number from five plots and from upper and lower soil layers). Each seedling found corresponds with a seed bank density of 15.92 seedlings per m^2. Only selected species (characteristic, endangered etc.) are shown. For the full table, see Appendix 4.1 and 4.2.

Locality code/species	**Kallmünz**								**Kaltes Feld**							
	K0	K15a	K15b	K40	K60	K90	K180a	K180b	F0	F8	F50a	F50b	F100	F153	F180a	F180b
Weeds and ruderals																
Anagallis arvensis	7	6	25	2	6	2			2			1	5	2		
Arenaria serpyllifolia	32			4					11	12	22	2				
Chenopodium album agg.	10	3	13	3	2	2			1	1		1				
Chaenorhinum minus	87				1	1			9	6	2	4	5	1		2
Veronica arvensis			20	5					2	41						
Veronica persica			1						71	1						
Digitaria ischaemum	177		2													
Thlaspi arvense			19													
Neslia paniculata			2													
Silene noctiflora			2													
Aphanes arvensis					1					1						
Sherardia arvensis									8							
Stachys annua											2					
Kickxia spuria												2				
Mesophilous species																
Poa angustifolia	1	28		10	13	13	23	4	5		2	5	20	29	1	3
Hypericum perforatum		1	92	12	40	19	2		2	15	115	114	19	29	21	2
Medicago lupulina		2	4		15	3	3	3		1	5	6	24	60	1	4
Daucus carota		2	56	1	1	5				1	1	7	7	5	6	14
Plantago lanceolata			23	3	1		1			20	1		6	4	8	10
Leucanthemum vulgare				1						3	27	9	1	3	1	41
Origanum vulgare											11	40	34		19	1
Xerophilous species																
Potentilla neumanniana		3		11	3		29	2					1	6	5	2
Carex caryophyllea				3	5		27	16			5	20	19	2	24	24
Linum catharticum					5		15	1			12	31	67	35	25	45
Phleum phleoides				2		17		2								
Cerastium brachypetalum			3	9												
Carex flacca											1	111	251	8	214	239
Thymus pulegioides s. str.											1	2	4	8	10	7

<u>*Seed bank in the Kaltes Feld region*</u>

Table 4.2 and Appendix 4.2 list the seed bank composition at the study site Kaltes Feld. The most common species as to the number of occurrences in particular plots were *Hypericum perforatum, Linum catharticum, Carex caryophyllea, Carex flacca, Medicago lupulina, Poa angustifolia, Origanum vulgare, Plantago lanceolata, Daucus carota* and *Trifolium repens.* The highest numbers of seedling individuals were found to belong to *Carex flacca, Hypericum perforatum, Linum catharticum, Origanum vulgare* and *Medicago lupulina.*

In the seed bank of recent grasslands, we discovered two rare species, which were completely missing aboveground: *Kickxia spuria* (F50b) and *Stachys annua* (F50a). Of uncommon grassland (or heliophilous forest) species, *Senecio erucifolius* (F180a, F100) and *Carex montana* (F180a), which both occurred also in aboveground vegetation, emerged rarely.

Comparison of seed banks at Kallmünz and Kaltes Feld

Species richness in the soil seed bank is slightly higher at Kallmünz (92 species) compared to Kaltes Feld (86 species). However, the total number of seedlings was more than two times higher at Kaltes Feld (2743 seedlings in total; 5457 seedlings/m^2) than at Kallmünz (1268 seedlings in total; 2523 seedlings/m^2). Also the total number of species occurrences present in particular samples (N=80 in each region; values were counted without regard for the quantity of species in each subplot) was higher at Kaltes Feld (734) compared to Kallmünz (457). There is no linear relationship between species richness and grassland age (Fig. 4.2). It is worth noting that the lowest number of species occurred at the beginning and at the end of the successional sere under study.

Figure 3 shows a relationship between soil seed bank density and age. However, this relationship is exactly opposite in the two regions. At Kallmünz seed bank density decreased with age whereas at Kaltes Feld it increased.

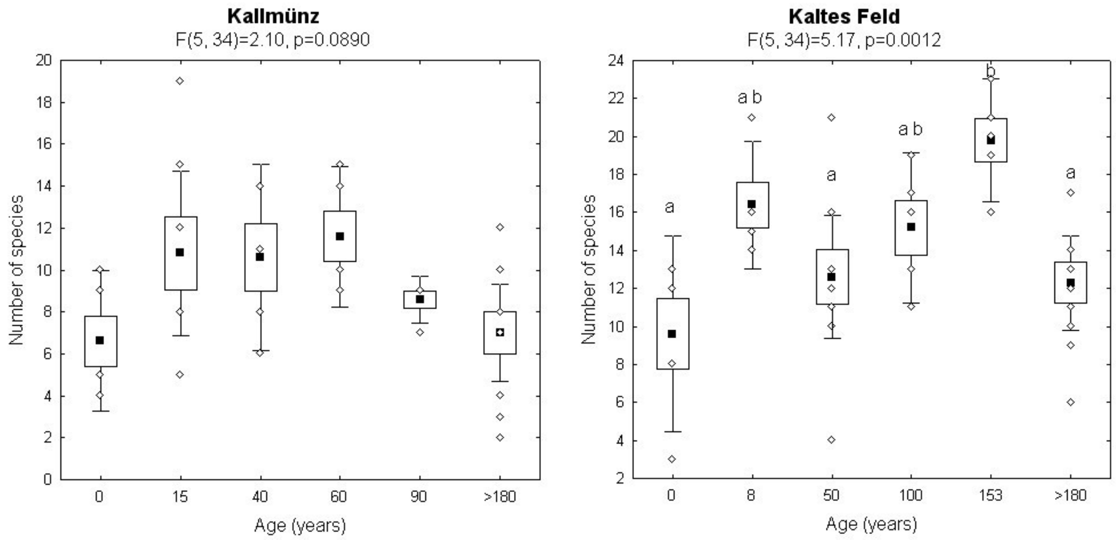

Fig. 4.2. – Numbers of species in the soil seed bank of arable fields and recent and ancient grasslands in Kallmünz (a) and Kaltes Feld (b). Boxes represent means and standard errors; whiskers show standard deviations (0.95 confidence interval). Rhombs mark raw data.

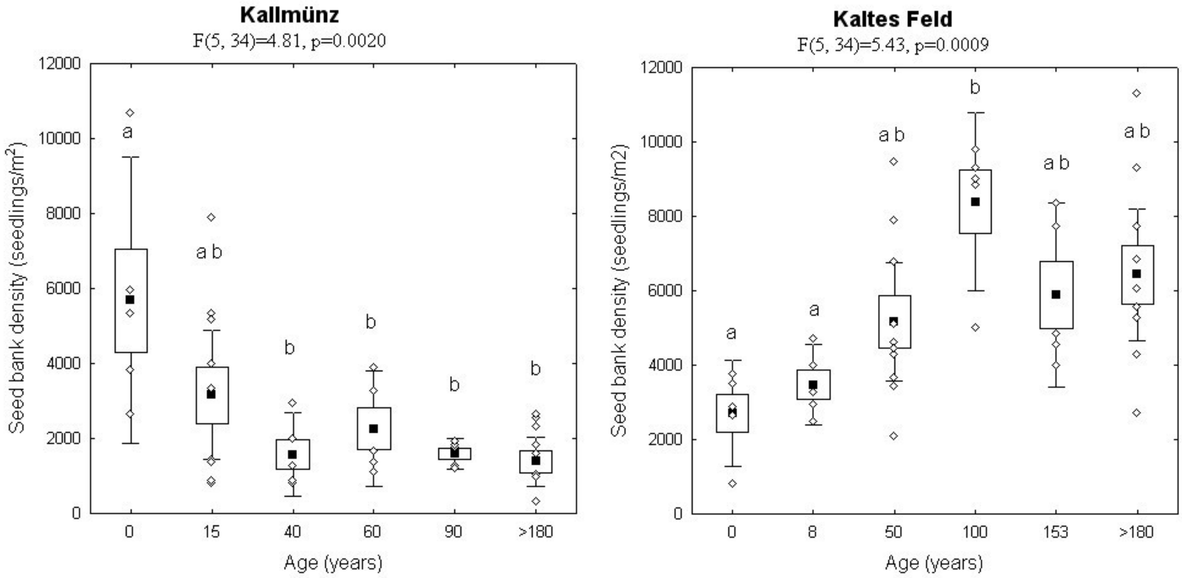

Fig. 4.3. – Soil seed bank density of arable fields and recent and ancient grasslands in Kallmünz (a) and Kaltes Feld (b). Boxes represent means and standard errors; whiskers show standard deviations (0.95 confidence interval). Rhombs mark raw data.

Proportion of ecological groups along the soil seed bank successional sere

Along the successional sere of the soil seed bank, every ecological group had a maximum in a different stage defined by the age of the grassland.

The highest proportion of dry grassland species in the soil seed bank was found in ancient grasslands (Table 4.3). Mesophilous grassland species were represented at all localities but with a maximum in recent grasslands. Species of both dry and mesophilous grasslands were nearly missing in both current fields in spite of their vicinity to neighbouring grasslands. Weedy and ruderal species (with the only exception of *Chaenorhinum minus*) were exclusively restricted to arable fields and recent grasslands, especially the youngest ones.

There was also a distinctive pattern of life forms along the soil seed bank successional sere (Table 4.3). The main group was formed by hemicryptophyte species which lost their dominance only in very young grasslands and in fields. The number of therophyte species decreased towards ancient grasslands. Chamaephytes were represented only by a few species, which, however, represented a regular part of soil seed banks of all grasslands older than 40 years.

Seed traits of seed bank species

Results of the analysis pointing to traits connected with reproduction by seeds are presented in Table 4.3. Although differences in average seed mass, size and shape were highly significant between the localities ($p<0.0001$), there was no clear and simple trend along the gradient of grassland age except for two seed characteristics measured without appendages. Ancient grassland species have on average longer and more elongated seeds in the soil seed bank than recent grasslands. Analysis of the longevity index shows a distinct decrease with increasing grassland age. This trend is especially evident in the upper soil layer, while in lower soil layer it is rather weak.

Ordination of seed banks

Ordination diagrams of an indirect analysis DCA show very clear patterns for both regions. Their first axes can be interpreted as grassland age (Fig. 4.4, 4.5).

The ordination diagram for Kallmünz shows arable field plots on the left side and ancient grassland plots on the right. The vertical distribution of recent grasslands on the second axis is not easily interpretable; nutrient content in the soil may have a certain importance. Soil seed bank composition is quite heterogenous (total inertia = 8.46), which can be ascribed to the specific soil seed bank composition of arable fields which differs substantially from the seed banks of recent grasslands.

In the ordination diagram of the Kaltes Feld ancient grassland, plots are situated on the left, arable field plots being on the right. Remarkable is the vertical distribution of recent grasslands in the middle of the diagram along the second axis, which can be interpreted using several environmental factors (geology, soil-reaction, solar radiation, etc.). At the top of the diagram, soil seed bank samples from 150 years old grasslands on a plateau built of hard reef limestone (F153) are found. Samples from grasslands on marlstone (F100) are in the middle; these are quite similar to ancient grassland seed banks. In the upper part of the diagram, there are young grasslands on rather steep, south-oriented slopes (F50a, F50b).

For Kallmünz, the ordination axis does not explain much variability (AX1 = 10.9 %, cumulative percentage variance explained by four axes = 23.2 %). By contrast, the soil seed bank from Kaltes Feld has lower variance (total inertia = 4.87), and the ordination axis explains more variability of the data set (AX1 = 17.0 %, cumulative percentage variance explained by four axes = 30.3 %).

To explain seed bank variability, we used the direct ordination method CCA. It identified three groups of variables with a strong and significant effect (tested using a Monte Carlo permutation test). Grassland age explained a high portion of variability. Further variability was explained by potential direct solar radiation on the 21th of June calculated using slope and aspect. Grassland biodiversity (expressed by species number in aboveground vegetation or Shannon-Wiener index of species richness) also had a significant influence, but it was autocorrelated with grassland age. Soil properties such as nutrient content or water holding capacity might be vastly important, but data were not available for every sample.

Comparison between vegetation and seed-bank

The number of species occurring in the soil seed bank and the vegetation is presented in Table 4.4. Especially at Kaltes Feld, there is a positive relationship between the number of species in the soil seed bank and the number of species in the vegetation; this correlation is not significant, however ($r=0.278$, $p=0.083$, $N=40$). The similarity between the seed bank and vegetation applying Sørensen´s index depends strongly on the scale of investigation. We therefore calculated the similarity for whole localities (five seed bank and vegetation plots were pooled, N=8, Table 4.3) and for single plots of 4 m^2 size (N = 40, Fig. 4.6).

It is evident from Appendix 4.1 and 4.2 that the majority of species from the soil seed bank also occurred in the vegetation. The exceptions were weeds (especially *Anagallis arvensis*, *Chaenorhinum minus*, *Chenopodium album* agg. and *Viola arvensis*), which occurred only in the seed bank or partly in the vegetation of current arable fields. On the other hand, many species occurring commonly in the vegetation were absent from the seed bank (see Appendix 4.3 and 4.4). These were typically woody species (notably *Prunus spinosa* and *Juniperus communis*), many grasses (especially *Avenula pratensis*, *A. pubescens*, *Festuca ovina* subsp. *guestfalica* and *F. rupicola*) and some other species (e.g. *Agrimonia eupatoria*, *Carlina* sp. div., *Centaurea rhenana*, *Cirsium acaule*, *Hieracium pilosella*, *Knautia arvensis* and *Vicia cracca* agg.).

Discussion

Total seed bank density and a possible climatic influence

Total seed bank densities in both studied regions roughly correspond to literary values for dry grasslands (Dutoit and Alard, 1995; Bisteau and Mahy, 2005, etc.; Appendix 4.5). The considerably higher seed bank density at Kaltes Feld compared to Kallmünz can be explained by the more oceanic climate at Kaltes Feld, where dry grasslands grow under more humid conditions. A comparison of published soil seed bank densities from different European grassland sites and types shows that the more continental and drier the grassland is, the lower its seed bank density. Mesophilous grasslands or wet meadows have, in most cases, higher soil seed bank densities (see Appendix 4.5). It is difficult, however, to precisely explain the mechanism causing this pattern because of the complex nature of interactions between climatic variables and seed production, longevity, dying, emergence, etc. (Walck et al., 2011; Poschlod et al., 2012). Recently, Abedi et al. (2013) showed that seed bank longevity depends on the interaction of soil moisture and substrate type and is even species-specific.

Effect of successional age on the seed bank density

In agreement with the literature (Soukupová, 1984; Fischer, 1987; Soukupová, 1990), the seed bank density of young successional stages at Kallmünz (K0, K15a, K15b) was higher than in old grasslands. The fact that young successional stages at Kaltes Feld (F0, F8) exhibit very low seed bank density is unexpected, however. It can be only explained by effective weed control (e.g. using herbicides) during the most recent farming practices.

Table 4.3. – Total species number in the soil seed bank, species number of specific phytosociological groups in the seed bank, species number of Raunkiaer plant life-forms in the seed bank, seed mass average, seed length, width, height, seed shape (0=sphere, 0.2=extremely elongated or flat), longevity index, percentage of species with transient, short-term persistent and long-term persistent seed bank, species number of aboveground vegetation (list from five plots in a locality) and Sørensen´s indices comparing the floristic composition of aboveground vegetation and seed bank at localities in the Kallmünz and Kaltes Feld regions studied. All results were calculated based on presence/absence data without any regard for the quantity of particular species. In all cases, with the exception of longevity, only results of analyses where both soil layers are pooled are shown.

Locality code/variable	Kallmünz								Kaltes Feld							
	K0	K15a	K15b	K40	K60	K90	K180a	K180b	F0	F8	F50a	F50b	F100	F153	F180a	F180b
Total number of species in the seed bank (N)	16	18	37	30	30	21	21	17	23	32	22	29	36	35	27	23
Phytosociological groups (N)																
Stellarietea mediae and *Artemisietea vulgaris*	14	7	23	7	9	5	0	0	19	22	4	6	4	6	0	1
Molinio-Arrhenatheretea	1	2	7	5	4	2	1	1	1	5	4	4	6	8	3	3
Festuco-Brometea and *Sedo-Scleranthetea*	0	3	2	9	9	10	13	14	0	1	8	10	14	10	13	10
Other species	1	6	5	9	8	4	7	2	3	4	7	14	12	11	12	9
Raunkiaer plant life-forms (N)																
therophytes	12	9	23	9	9	5	2	1	16	16	4	8	4	4	1	2
geophytes	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0
hemicryptophytes	4	9	12	19	20	16	16	13	7	14	17	24	30	28	25	20
chamaephytes	0	0	0	2	1	0	3	3	0	0	2	2	2	2	2	1
Seed mass average (mg)	1.07	0.92	2.04	0.67	2.48	3.21	1.07	1.49	1.13	1.65	1.30	0.75	0.98	0.96	1.14	0.88
Seed length average (mm)																
with appendages	3.52	3.12	2.81	2.47	2.31	2.17	1.93	2.53	5.23	4.23	2.15	1.87	2.22	2.04	2.48	2.18
without appendages	1.73	1.59	1.86	1.65	1.92	1.87	1.82	2.21	1.89	2.33	2.03	1.75	1.99	1.91	2.21	2.06
Seed widht average (mm)																
with appendages	1.40	1.47	1.50	1.15	1.41	1.28	1.23	1.24	1.95	1.53	1.27	1.21	1.21	1.17	1.29	1.08
without appendages	0.90	1.07	1.23	1.09	1.31	1.16	1.20	1.11	1.10	1.45	1.23	1.14	1.08	1.13	1.11	1.04
Seed height average (mm)																
with appendages	0.75	0.75	1.00	0.71	0.93	0.95	0.82	0.83	1.28	1.06	0.82	0.77	0.86	0.81	0.89	0.75
without appendages	0.86	0.82	0.97	0.69	0.82	0.84	0.81	0.74	0.82	0.98	0.81	0.74	0.76	0.79	0.75	0.73
Seed shape average (0.0–0.2)																
with appendages	0.087	0.079	0.068	0.074	0.064	0.068	0.060	0.082	0.075	0.068	0.070	0.064	0.074	0.068	0.076	0.076
without appendages	0.069	0.067	0.078	0.063	0.063	0.065	0.058	0.077	0.063	0.061	0.066	0.062	0.074	0.065	0.077	0.072
Longevity index average																
both soil layers are pooled	0.74	0.68	0.63	0.54	0.54	0.65	0.49	0.33	0.74	0.71	0.53	0.56	0.50	0.54	0.41	0.48
upper soil layer	0.75	0.67	0.65	0.52	0.48	0.63	0.49	0.29	0.73	0.69	0.53	0.57	0.49	0.53	0.40	0.47
lower soil layer	0.73	0.70	0.65	0.73	0.66	0.80	0.51	0.49	0.71	0.72	0.61	0.55	0.60	0.57	0.55	0.57
Longevity (%N)																
transient	0.0	16.7	11.1	33.3	23.3	22.2	25.0	66.7	4.3	0.0	13.6	17.6	33.3	15.2	46.4	34.8
short-term persistent	26.7	38.9	27.8	37.0	36.7	22.2	45.0	6.7	30.4	33.3	40.9	35.3	30.6	45.5	28.6	30.4
long-term persistent	73.3	44.4	58.3	29.6	40.0	55.6	30.0	20.0	65.2	66.7	45.5	47.1	36.1	39.4	25.0	34.8
Total number of species in the aboveground vegetation (N)	16	44	35	70	60	39	50	47	34	36	66	66	66	73	60	52
Sørensen´s similarity index	0.35	0.29	0.31	0.46	0.47	0.53	0.48	0.53	0.53	0.37	0.38	0.48	0.55	0.54	0.57	0.45

Similarity between the seed bank and aboveground vegetation

Very recent grasslands (K15a, K15b, F8) show the lowest similarity between aboveground vegetation and the soil seed bank – the older the grasslands, the higher the similarity between the vegetation and the soil seed bank. This is due to the relatively faster succession of aboveground vegetation compared to the soil seed bank. Although grassland species are already present in the aboveground vegetation in very recent grasslands, the soil seed bank is still dominated by weeds and species of youngest fallows. This may also be partly explained by the fact that many mesophilous species of this successional stage have no persistent seed bank at all (Bekker et al., 1997; 1998a). By contrast, current arable fields and older recent grasslands exhibit a relatively high similarity between their aboveground vegetation and soil seed bank. In arable fields, this is due to strong selection for short-lived species with efficient generative reproduction, which occur in both aboveground vegetation and the soil seed bank. In the case of older recent grasslands, this is caused by the depletion of the seed bank of many arable weeds, which disappear from the vegetation shortly after the cessation of arable use. The similarity is, again, lower in ancient grasslands because most calcareous grassland species do not have a persistent seed bank (Bekker et al., 1998a; Poschlod et al., 1998).

At Kaltes Feld, the higher similarity between aboveground vegetation and the seed bank (Fig. 4.6) may be ascribed to the larger seed bank in this region (Fig. 4.2) and therefore a higher probability of species occurring in the vegetation as well as in the seed bank.

Similarity indices are either consistent with values reported in the literature (Soukupová, 1990; Dutoit and Alard, 1995) or higher (Bisteau and Mahy, 2005). However, only Willems (1995) reports substantially higher values (Sørensen´s index = 0.77), which may be because of very intensive seed bank sampling in permanently marked plots of 1 m^2, resulting in a larger seed bank species list and therefore higher similarity with aboveground vegetation.

Our data confirm the fact that soil seed bank dynamics are much slower than vegetation dynamics (Bekker et al., 2000; Bisteau and Mahy, 2005). The most stable factor is the soil seed bank of weeds, although these species are already missing in the vegetation for longer time periods (Chippindale and Milton, 1934; Kretzschmar, 1994). Weeds in the soil seed bank are in any case a good indicator of the status of a grassland; their presence indicates a recent grassland whereas their absence indicates an ancient one.

Some species found in the soil seed bank are relics of former crops. Seeds of rape (*Brassica napus*) are a typical example. Other examples are *Trifolium hybridum, T. pratense* subsp. *sativum, Phleum pratense* and probably *Vicia sativa* s.l., which were used to be sown to produce fodder (e.g. Veith, 1813; Martens and Kemmler, 1865). The occurrence of *Alopecurus pratensis* and *Phleum pratense* in the seed bank of arable fields can also be explained by an influx of seeds through manuring (after having been used as litter or fodder in the stable; Bonn and Poschlod, 1998).

Table 4.4. – Number of species occurring in the seed bank and aboveground vegetation.

Kallmünz (total: 168 species in seed bank and/or vegetation)		Seed-bank 92	
		Absent	Present
Vegetation 142	Absent	-	27
	Present	77	65
Kaltes Feld (total: 181 species in seed bank and/or vegetation**)**		Seed-bank 87	
		Absent	Present
Vegetation 162	Absent	-	19
	Present	94	68

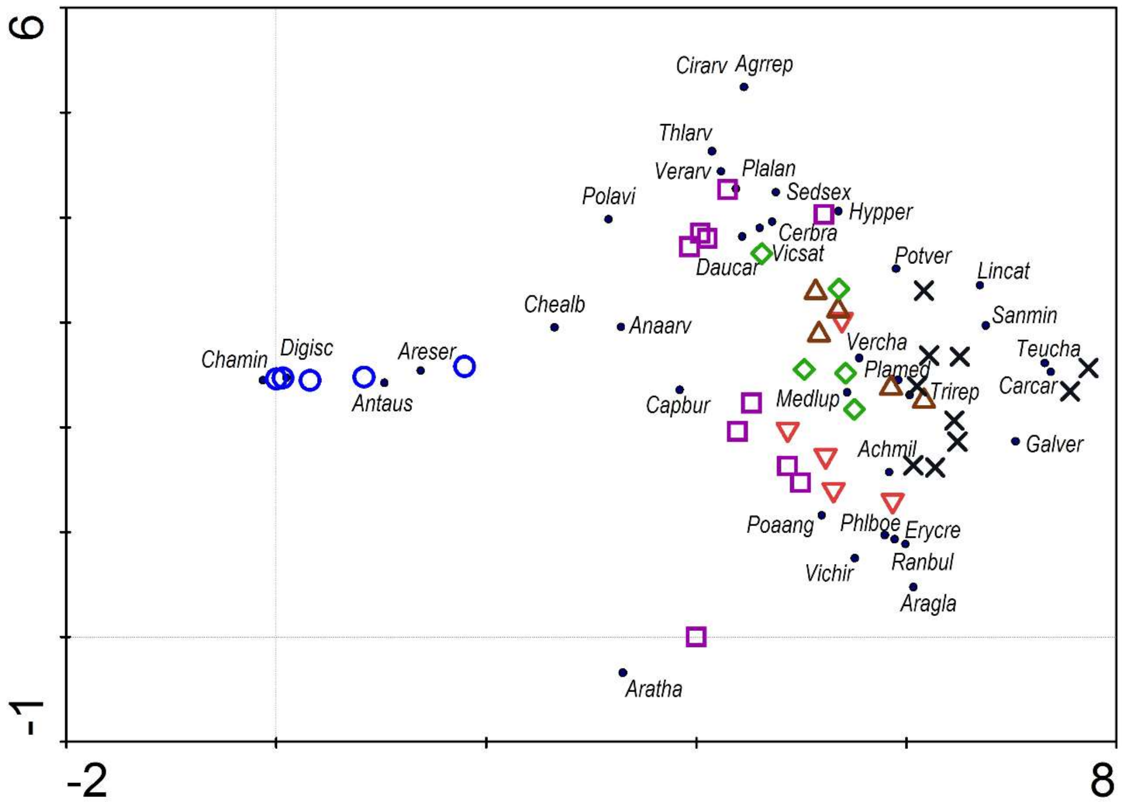

Fig. 4.4. – Ordination diagram of a detrended correspondence analysis (DCA) of all plots in Kallmünz showing species composition of the soil seed bank in grasslands of different age. Grassland age categories: X-mark = ancient, down-triangle = 90 years, up-triangle = 60 years, diamond = 40 years, square = 15 years, circle = current field. Only the 43 most correlated species (species fit range > 2%, small circles) are presented. For the full species names, see Appendix 4.1.

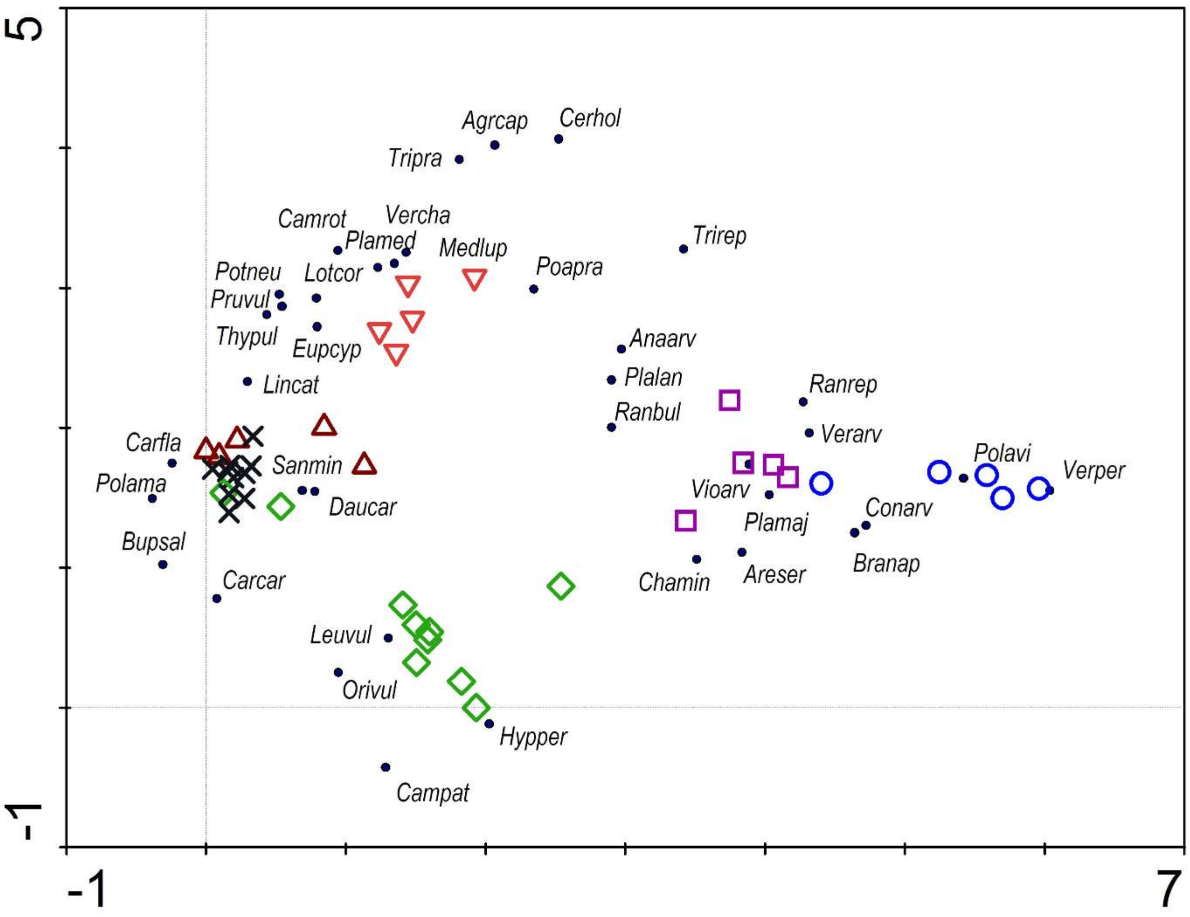

Fig. 4.5. – Ordination diagram of a detrended correspondence analysis (DCA) for Kaltes Feld showing species composition of the soil seed bank in grasslands of different age. Grassland age categories: X-mark = ancient, down-triangle =153 years, up-triangle = 100 years, diamond = 50 years, square = 8 years, circle = current field. Only the 39 most correlated species (species fit range > 1%, small circles) are presented. For the full species names, see Appendix 4.2.

<u>*Soil seed bank persistence and vertical structure of seed bank*</u>

The most exact way to assess seed bank longevity of individual species is by long-term seed viability experiments, but these are still scarce (Telewski and Zeevaart, 2002). The most common approach to assessing seed bank longevity is therefore extraction of data from seed bank databases (Thompson et al., 1997; 1998), even though this approach has recently been criticized by Saatkamp et al. (2009). Our study on grasslands of known age offers the possibility to test its reliability at least for weeds and ruderals. Our results generally match the general classification of seed longevity provided by trait databases.

In the seed banks of younger successional stages, weedy and ruderal species commonly occur together with a certain number of mesophilous grassland species (see Appendix 4.1 and 4.2). Many weedy and ruderal species have high seed longevity, which has already been shown in numerous studies (Priestley, 1986; Thompson et al., 1997; Bekker et al., 1998a; Poschlod et al., 2005; 2012). On the contrary, typical dry grassland species mostly have transient or short-term persistent seed banks (Thompson et al., 1997). Seed bank composition of samples from younger successional stages therefore exhibits a markedly higher average value of the longevity index (Table 4.3).

Good examples of species with short seed germinability that are very abundant and dominant in vegetation but very rare in seed bank are *Brachypodium pinnatum* and *Fragaria viridis* (Poschlod et al., 1998). On the other hand, certain long-term persistent species growing in aboveground vegetation are at the same time missing in the seed banks of particular localities (e.g. *Arabis hirsuta*, *Euphorbia helioscopia*, *Fumaria officinalis*), but their absence from the seed bank is explainable by their very low abundance in vegetation producing only a limited number of seeds.

Concordantly, the presence of certain dry grassland species and the absence of weedy species in the soil seed bank indicate the state of ancient grasslands. Lower seed longevity of typical dry grassland species on the one hand and higher seed longevity of weedy and ruderal species on the other also explain the lower number of species and seedlings emerging from the soil seed bank in ancient grasslands compared to recent grasslands.

Germinable seeds of weeds in the soil seed bank as remnants of previous arable field use indicate the recent status of the habitat. These habitats can be of different age, as has been well documented along successional seres from croplands to mature forests (e.g. Brenchley, 1918; Oosting and Humphreys, 1940; Livingston and Allessio, 1968).

Despite the fact that most weedy species such as *Anagallis arvensis* will never establish or even reproduce in grasslands, we found their living seeds in the seed bank decades after arable fields were abandoned and converted into grasslands. This means that seeds of certain species of the previous arable stage are able to survive for a long time, even for longer than 150 years. On the other hand, as our results show, seeds of arable weeds do not survive forever. Only a few of them were present in the oldest recent grasslands (F153, K90).

Most species and most seeds occur in the upper soil layer (e.g. *Medicago lupulina, Plantago lanceolata, Euphorbia cyparissias*), indicating a transient or only short-term persistent seed bank. Some typical dry grassland species with strongly limited longevity, namely *Anthyllis vulneraria*, *Brachypodium pinnatum*, *Dianthus carthusianorum* and *Globularia bisnagarica,* occur exclusively in the upper soil layer.

Weeds like *Anagallis arvensis* and *Viola arvensis* occur rather in deeper soil layers (see Appendix 4.1 and 4.2), indicating a long-term persistent seed bank (Bekker et al., 1998a). This fact is also documented by Kiirikki (1993) who studied 21-year-old fallows of arable fields in southern Finland. The depletion of upper soil layers can be simply explained by the fact that weeds may germinate but do not establish and reproduce in a dense sward. The effect of accelerated depletion of weedy species in upper soil layers is well documented by the average longevity index calculated for the whole species spectrum at each locality (Table 4.3). Thus the decrease of average longevity depending on grassland age is more rapid in the upper than in the lower soil layers.

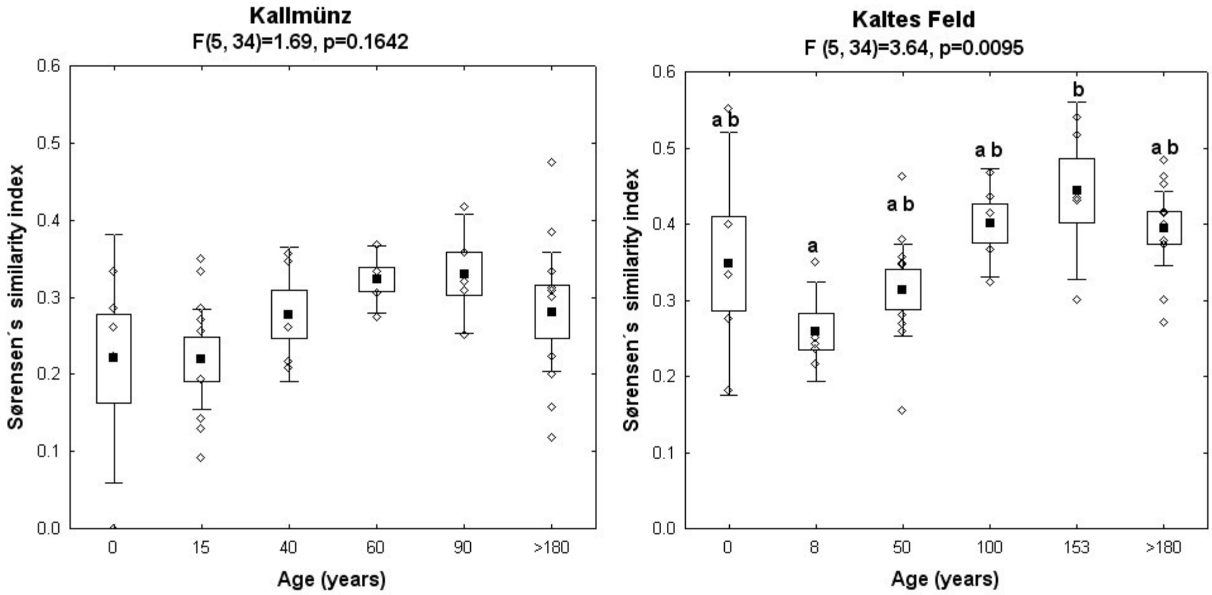

Fig. 4.6. – Similarity between the seed bank and vegetation in Kallmünz (a) and Kaltes Feld (b) calculated using Sørensen´s index and its dependence on grassland age. Similarity indices were calculated for single plots of 4 m^2 size (N = 40).

Seed traits and age of grassland

We have already shown that seed longevity significantly decreases with grassland age (Table 4.3). Long-term persistent seeds are generally expected to be small and spherically shaped, and vice versa (Thompson et al., 1993; Schwienbacher et al., 2010; Zhao et al., 2011). Our results are nonetheless only in partial agreement with this expectation. Only if seeds are measured without appendages is there an observable increase in the length of seeds and a change in their shape (seeds are less spheric) along the successional gradient, meaning that long-term persistence of seeds in the soil seed bank decreases with grassland age (Bekker et al., 1998).

Relevance of the soil seed bank for the protection of rare species

The low importance of dry grassland soil seed banks for habitat restoration and their low ability to buffer the extinction of rare species was already described by Poschlod et al. (1998) and Stöcklin and Fischer (1999). However, this is only true for ancient grassland indicators. In contrast to ancient grasslands, the soil seed bank of recent grasslands may have a high importance for the conservation of rare weeds. Some of these weeds may even be locally extinct, in this case for example, *Kickxia spuria*, *Silene noctiflora* and *Stachys annua*. *Stachys annua* has not been observed in the Kaltes Feld region and its surroundings for several decades (Alexejew et al., 1988; Rodi, 1988). The importance of the soil seed bank of recent grasslands for seed storage of rare arable weeds such as *Althaea hirsuta* was recently recognized also by Forey and Dutoit (2012). Populations of these species are still declining despite many conservation management programmes aimed at their preservation, for example, by leaving strips along field edges where no fertilizers and herbicides are applied (Otte et al., 1988; 2006). Highly intensive farming in the last decades has even caused these species to disappear from the seed banks of arable fields (Schneider et al., 1994; Schumacher and Schick, 1998).

Weed seeds may live under grassland use for much longer than under conventional arable field use, which leads to depletion of the seed bank by ploughing and through the application of herbicides.

The protection of the soil seed banks of rare species is therefore another aspect of soil conservation, which should definitely not be ignored. This has already been shown and discussed for other habitats subjected to management changes such as ponds. Despite the abandonment of traditional periodic emptying during the vegetation period, seeds of highly threatened and even regionally extinct species may still be found in high quantities in pond mud after decades or even after more than hundred years (Poschlod, 1993b; 1999; Poschlod et al., 1996; Bernhardt et al., 2004; 2005).

Finally, ploughing of recent grasslands without the use of subsequent agricultural techniques such as herbicide application may be an appropriate management method for re-establishment and maintenance of rare weedy species by activating and refreshing the seed bank. However, management of NATURA 2000 sites is often subjected to the "iron rule" of the Habitat Directive, which aims to ensure the maintenance or restoration of natural habitats and the protection of species enjoying Community interest at a favourable conservation status. In our opinion, matters should be handled in a more flexible way to allow changes of land use as long as each change represents only a kind of disturbance regime but no fertilization or any other method of intensive conventional arable field use. Ploughing of recent grasslands may be a good management tool not only for restoring endangered weed communities but also for helping dry grasslands themselves. Ploughing creates younger successional stages of grasslands, which host disturbance-dependent threatened species such as *Gentiana cruciata* (Poschlod et al., 2008). Such actions must be well reasoned and documented, of course.

Conclusion

Soil seed banks in calcareous grasslands hold information on the history of past land use. In this study, we were able to detect former arable cultivation after more than a century.

There are qualitative rather than quantitative differences between the soil seed banks of recent and ancient grasslands. Seeds of arable weeds may persist especially in the soil seed bank of recent grasslands over a long term. By contrast, seeds from arable weed species are completely missing from the seed banks of ancient grasslands.

Soil seed banks have only a limited significance for the restoration of species-rich calcareous grasslands. That the soil seed banks of recent grasslands store seeds of rare weed species which otherwise do not occur in current grasslands and fields is nevertheless of great conservation importance.

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Appendix 4.1. – Composition of the seed bank of the Kallmünz region. The table presents numbers of seedlings in the upper and lower soil layers and their sum (in bold) for eight localities analysed. Each seedling found (sum of both depths) corresponds with a seed bank density of 15.92 seedlings per m^2. The second column contains species abbreviations used in ordination diagrams. The presence of a species in both the seed bank and aboveground vegetation at a locality is indicated by an italicized seedling number and grey background.

Locality code		K180a			K180b			K90			K60			K40			K15a			K15b			K0		
Aliance *Bromion erecti*																									
Linum catharticum	Lincat	15	12	3	1		1				5	4	1												
Sanguisorba minor	Sanmin	5	5					1	1		1		1	1	1										
Euphorbia cyparissias	Eupcyp	1	1					2	2		1	1													
Helianthemum nummularium s.l.	Helova	2	2		2	2																			
Phleum phleoides	Phlboe				2	2		17	14	3				2	2										
Fragaria viridis	Fravir	1	1								1	1													
Brachypodium pinnatum	Brapin				1	1																			
Anthyllis vulneraria	Antvul				2	2																			
Koeleria pyramidata	Koepyr										2	2													
Polygala comosa	Polcom										1	1													
Other xerophilous species																									
Potentilla neumanniana	Potneu	29	19	10	2	1	1				3	3		11	9	2	3	2	1						
Carex caryophyllea	Carcar	27	18	9	16	8	8				5	5		3	3										
Galium verum	Galver	1	1		2	2		1	1		1	1		1	1										
Medicago falcata	Medfal	2	2		1		1	1	1																
Teucrium chamaedrys	Teucha	5	4	1																					
Teucrium montanum	Teumon	2	1	1																					
Cerastium glomeratum	Cerglo	1	1																	2	2				
Arabis hirsuta	Arahir	1	1																						
Securigera varia	Secvar				2	1	1	1	1																
Chamaecytisus ratisbonensis	Charat				2	1	1																		
Potentilla cinerea	Potcin				1		1							2	2										
Dianthus carthusianorum	Diacar				1	1																			
Globularia bisnagarica	Globis				1	1																			
Arabis glabra	Aragla							10	6	4															
Erysimum crepidifolium	Erycre							7	4	3															
Inula conyza	Inucon							4	4																
Centaurea rhenana	Cenrhe							1	1																
Cerastium brachypetalum	Cerbra													9	8	1				3	3				
Sedum sexangulare	Sedsex													5	4	1									
Myosotis stricta	Myostr													1	1										
Saxifraga tridactylites	Saxtri																3	2	1						
Potentilla argentea	Potarg																1	1							
Alliances *Bromion* and *Arrhenatherion*																									
Poa angustifolia	Poaang	23	13	10	4	3	1	13	12	1	13	9	4	10	7	3	28	25	3				1		1
Plantago media	Plamed	4	4								8	8		7	7		1		1						
Ranunculus bulbosus	Ranbul	3	2	1							3	3					1	1							
Lotus corniculatus	Lotcor										2	2													
Pimpinella saxifraga	Pimsax													3	3										
Salvia pratensis	Salpra													1	1										
Alliance *Arrhenatherion elatioris*																									
Plantago lanceolata	Plalan	1	1								1	1		3	3					23	23				
Achillea millefolium	Achmil				1	1		2	2		1	1					1	1		1	1				
Daucus carota	Daucar							5	3	2	1	1		1		1	2	2		56	40	16			
Veronica chamaedrys	Vercha										17	17		1	1										
Leucanhmum vulgare	Leuvul													1		1									

Trifolium pratense	Tripra																			***3***	*3*				
Arrhenatherum elatius	Arrela																			***1***		*1*			
Class *Molinio-Arrhenatheretea*																									
Cerastium holosteoides	Cerhol														***1***	*1*									
Trifolium hybridum	Trihyb																			**2**	2				
Phleum pratense	Phlpra																			***1***	*1*		**1**	1	
Weeds and ruderals																									
Anagallis arvensis	Anaarv							**2**	1	1	**6**	2	4	**2**		2	**6**	1	5	**25**	7	18	**7**	2	5
Chenopodium album agg.	Chealb							**2**	1	1	**2**	1	1	**3**		3	**3**	2	1	**13**	8	5	**10**	5	5
Vicia sativa s.l.	Vicsat							**1**	1		**1**	1								***3***	*2*	*1*			
Vicia hirsuta	Vichir							***3***	*3*		***1***	*1*					***2***	*2*							
Chaenorhinum minus	Chamin							**1**		1	**1**	1											**87**	40	47
Viola arvensis	Vioarv										**3**		3							**1**		1			
Linaria vulgaris	Linvul										**2**	2													
Polygonum aviculare	Polavi										**1**	1								**5**	4	1	**2**		2
Aphanes arvensis	Apharv										**1**		1												
Veronica arvensis	Verarv													**5**	5					**20**	17	3			
Arenaria serpyllifolia	Areser													***4***	*3*	*1*							***32***	*22*	*10*
Arabidopsis thaliana	Aratha													**1**	1		**12**	8	4	**2**		2	**3**	1	2
Valerianella locusta	Valloc													***1***		*1*				**1**	1				
Poa compressa	Poacom													**1**		1									
Capsella bursa-pastoris	Capbur																**4**	4		**6**	2	4	***1***	*1*	
Torilis japonica	Torjap																**1**	1							
Erophila verna	Erover																**1**		1						
Thlaspi arvense	Thlarv																			**19**	13	6			
Cirsium arvense	Cirarv																			**15**	10	5			
Agropyron repens	Agrrep																			***5***	*3*	2			
Neslia paniculata	Nespan																			**2**	2				
Fallopia convolvulus	Falcon																			**2**		2			
Silene noctiflora	Silnoc																			**2**	2				
Echinochloa crus-galli	Echcru																			**1**	1				
Veronica persica	Verper																			**1**	1				
Setaria viridis	Set vir																			**1**	1				
Euphorbia helioscopia	Euphel																			**1**	1				
Tripleurospermum inodorum	Triino																			**1**		1			
Digitaria ischaemum	Digisc																			**2**	1	1	**177**	93	84
Plantago major	Plamaj																			**2**	1	1	**1**		1
Matricaria recutita	Matrec																			**1**		1	**1**	1	
Anthemis austriaca	Antaus																						***28***	*22*	*6*
Stellaria media	Stemed																						***3***	*3*	
Convolvulus arvensis	Conarv																						**2**	*1*	*1*
Lapsana communis	Lapcom																						**1**	1	
Other species																									
Hypericum perforatum	Hypper	***2***	*2*					***19***	*14*	*5*	***40***	*21*	*19*	**12**	*5*	*7*	**1**	1		**92**	81	11			
Medicago lupulina	Medlup	***3***	*2*	*1*	***3***	*1*	*2*	***3***	*3*		***15***	*13*	*2*				***2***	*2*		***4***	*4*				
Trifolium repens	Trirep	**1**		1							**2**	1	1	***3***	*2*	*1*				***2***	*1*	*1*			
Luzula campestris	Luzcam	**1**	1																						
Silene vulgaris	Silvul							***4***	*4*																
Carex muricata agg.	Carmur										***1***	*1*		***1***		*1*									
Potentilla reptans	Potrep													***1***		*1*									
Trifolium campestre	Tricam													***2***	*2*		***1***		*1*	***1***	*1*				
Trifolium pratense subsp. *sativum*	Trisat																			***1***		*1*			
Number of seedlings		**130**	93	37	**44**	27	17	**100**	79	21	**142**	105	37	**99**	72	27	**73**	55	18	**323**	239	84	**357**	193	164
Number of species		**21**	20	9	**17**	14	9	**21**	20	9	**30**	27	10	**30**	22	15	**18**	15	9	**37**	30	21	**16**	13	11

Appendix 4.2. – Composition of the seed bank of Kaltes Feld. The table presents numbers of seedlings in the upper and lower soil layers and their sum (in bold) for eight analysed localities. Each seedling found (sum of both depths) corresponds with a seed bank density of 15.92 seedlings per m^2. The second column contains species abbreviations used in ordination diagrams. The presence of a species in both the seed bank and aboveground vegetation at a locality is indicated by an italicized seedling number and grey background.

Locality code		F180a			F180b			F153			F100			F50a			F50b			F8			F0		
Aliance *Bromion erecti*																									
Linum catharticum	Lincat	***25***	*18*	*7*	***45***	*38*	*7*	***35***	*14*	*21*	***67***	*48*	*19*	***12***	*11*	*1*	***31***	*22*	*9*						
Sanguisorba minor	Sanmin	***12***	*9*	*3*				***8***	*8*		***1***		*1*	***6***	*6*		***6***	*6*							
Euphorbia cyparissias	Eupcyp				***3***	*1*	*2*	***5***	*3*	*2*	***10***	*9*	*1*				***2***	*2*							
Hippocrepis comosa	Hipcom	***1***	*1*								***1***	*1*		***1***	*1*										
Viola hirta	Viohir	***6***	*5*	*1*	***1***	*1*					***1***	*1*													
Brachypodium pinnatum	Brapin	***1***	*1*		***1***	*1*																			
Buphthalmum salicifolium	Bupsal	***10***	*10*																						
Thymus pulegioides subsp. *carniolicus*	Thycar							***4***	*3*	*1*															
Other xerophilous species																									
Carex caryophyllea	Carcar	***24***	*16*	*8*	***24***	*10*	*14*	***2***	*1*	*1*	***19***	*10*	*9*	***5***	*4*	*1*	***20***	*17*	*3*						
Carex flacca	Carfla	***214***	*183*	*31*	***239***	*144*	*95*	***8***	*7*	*1*	***251***	*176*	*75*	***1***	*1*		***111***	*101*	*10*						
Thymus pulegioides subsp. *pulegioides*	Thypul	***10***	*9*	*1*	***7***	*3*	*4*	***8***	*6*	*2*	***4***	*3*	*1*	***1***	*1*		***2***	*2*							
Polygala amarella	Polama	**1**	1		**1**	1					***7***	*7*		**1**	1										
Potentilla neumanniana	Potneu	***5***	*5*		**2**	2		***6***	*5*	*1*	***1***		*1*												
Senecio erucifolius	Seneru	***2***	*2*								***1***	*1*													
Carex montana	Carmon	***1***	*1*																						
Senecio jacobaea	Senjac				**1**	1		***1***	*1*																
Scabiosa columbaria	Scacol							***2***	*2*		***1***	*1*													
Inula conyza	Inucon										**1**	1					***1***	*1*							
Arabis hirsuta	Arahir										**1**		1	***3***	*3*		***2***	*2*							
Sedum acre	Sedacr																**1**		1						
Ajuga genevensis	Ajugen																***3***	*2*	*1*	***2***	*2*				
Alliances *Bromion* and *Arrhenatherion*																									
Poa angustifolia	Poaang	***1***	*1*		***3***	*1*	*2*	***29***	*18*	*11*	***20***	*16*	*4*	***2***	*2*		***5***	*2*	*3*				**5**	2	3
Ranunculus bulbosus	Ranbul	***3***	*3*					***2***	*2*		***3***	*3*					***1***		*1*	**5**	5				
Lotus corniculatus	Lotcor	***1***	*1*		***1***	*1*		***11***	*9*	*2*	***9***	*9*		***2***	*2*		***1***	*1*							
Centaurea jacea	Cenjac	***5***	*5*								***3***	*3*													
Pimpinella saxifraga	Pimsax	***1***	*1*								***1***	*1*													
Plantago media	Plamed				***1***		*1*	***9***	*5*	*4*	***3***		*3*	***1***	*1*		***2***		*2*						
Alliance *Arrhenatherion elatioris*																									
Plantago lanceolata	Plalan	***8***	*8*		***10***	*8*	*2*	***4***	*3*	*1*	***6***	*6*		***1***	*1*					***20***	*14*	*6*			
Leucanthemum vulgare s.l.	Leuvul	***1***	*1*		***41***	*28*	*13*	***3***	*2*	*1*	***1***		*1*	***27***	*16*	*11*	***9***	*9*		***3***	*3*				
Daucus carota	Daucar	***6***	*5*	*1*	***14***	*8*	*6*	***5***	*1*	*4*	***7***	*6*	*1*	***1***		*1*	***7***	*5*	*2*	***1***	*1*				
Veronica chamaedrys	Vercha							***9***	*6*	*3*	***4***	*3*	*1*				***3***	*1*	*2*						
Agrostis capillaris	Agrcap							***19***	*15*	*4*	**4**	4													
Trifolium pratense	Tripra							***12***	*8*	*4*															
Galium mollugo s.l.	Galmol										***2***	*2*													
Campanula patula	Campat																**30**	21	9						
Class *Molinio-Arrhenatheretea*																									
Anthoxanthum odoratum	Antodo							***1***	*1*																
Cerastium holosteoides	Cerhol							***24***	*21*	*3*										***2***	*2*				
Trifolium hybridum	Trihyb													**1**	1										
Ranunculus repens	Ranrep																			***13***	*12*	*1*			

Alopecurus pratensis	Alopra																						7	3	4
Weeds and ruderals																									
Chaenorhinum minus	Chamin				2	1	1	1	1		5	2	3	2	2		4	1	3	6	4	2	9	3	6
Anagallis arvensis	Anaarv							2	1	1	5	1	4				1		1				2	2	
Stachys alpina	Staalp							4	1	3										2		2			
Viola arvensis	Vioarv							1		1	1		1				1	1		7	3	4	1		1
Urtica dioica	Urtdio							1	1																
Poa compressa	Poacom										1		1												
Arenaria serpyllifolia	Areser													22	13	9	2	2		12	12		11	6	5
Convolvulus arvensis	Conarv													1	1					9	2	7	3	1	2
Stachys annua	Staann													2	1	1									
Chenopodium album s.str.	Chealb																1		1	1		1	1	1	
Kickxia spuria	Kixspu																2		2						
Veronica arvensis	Verarv																			41	36	5	2	1	1
Brassica napus subsp. *napus*	Branap																			14	6	8	5		5
Myosotis arvensis	Myoarv																			6	5	1	2	1	1
Polygonum aviculare subsp. *rurivagum*	Polavi																			3	1	2	12	5	7
Veronica persica	Verper																			1	1		71	39	32
Valerianella dentata	Valden																			2	2		2		2
Rumex obtusifolius	Rumobt																			1	1		1		1
Stellaria media	Stemed																			1		1	4	1	3
Fallopia convolvulus	Falcon																			5	1	4			
Galeopsis tetrahit	Galtet																			4	1	3			
Polygonum sp. (non *aviculare*)	Polsp.																			3	1	2			
Plantago major	Plamaj																			14	14				
Agropyron repens	Agrrep																			2	2				
Lapsana communis	Lapcom																			2	2				
Thlaspi arvense	Thlarv																			1	1				
Aphanes arvensis	Apharv																			1		1			
Sherardia arvensis	Shearv																						8	5	3
Capsella bursa-pastoris	Capbur																						7	1	6
Poa annua	Poaann																						6	3	3
Sonchus arvensis	Sonarv																						3		3
Galinsoga quadriradiata	Galqua																						1	1	
Other species																									
Hypericum perforatum	Hypper	21	13	8	2	2		29	21	8	19	13	6	115	55	60	114	83	31	15	13	2	2	2	
Medicago lupulina	Medlup	1		1	4	3	1	60	46	14	24	12	12	5	3	2	6	6		1	1				
Origanum vulgare	Orivul	19	16	3	1		1				34	26	8	11	6	5	40	24	16						
Prunella vulgaris	Pruvul	2	2		6	5	1	6	3	3	4	3	1				4	2	2						
Campanula rotundifolia	Camrot	6	5	1	3	2	1	32	20	12	3	3													
Galium pumilum	Galpum	1	1		1	1		2	2																
Trifolium repens	Trirep							19	13	6	2		2				1	1		18	15	3	5	3	2
Luzula campestris	Luzcam							5	4	1															
Rubus cf. idaeus	Rubida							1	1																
Potentilla reptans	Potrep													6	3	3	2	1	1						
Clinopodium vulgare	Clivul	7	7														2	2							
Trifolium campestre	Tricam																2	2							
Trifolium medium	Trimed																1		1						
Briza media	Brimed																1	1							
Number of seedlings		388	323	65	413	262	151	370	255	115	527	371	156	223	132	91	413	314	99	218	163	55	170	80	90
Number of species		27	26	11	23	21	15	35	34	26	36	28	22	22	21	9	29	23	18	32	28	18	23	18	19

Appendix 4.3. – List of species present in the vegetation which were not found in the seed bank at individual localities in the Kallmünz study region. The species list of aboveground vegetation for each locality resulted from five pooled 2×2 m vegetation plots and was compared with the list of species present in the seed bank of the given locality. Species are listed in alphabetical order. Additional information regarding the occurrence at individual localities is given in brackets.

Acinos arvensis (K40), *Agrimonia eupatoria* (K90, K60, K15b), *Agropyron repens* (K15a, K0), *Achillea millefolium* (K180a, K40), *Ajuga genevensis* (K15b), *Allium oleraceum* (K15a), *Alyssum montanum* (K90), *Aphanes arvensis* (K0), *Arabis hirsuta* (K40), *Arenaria serpyllifolia* (K180a, K90), *Arrhenatherum elatius* (K90, K60, K40, K15a), *Artemisia vulgaris* (K60, K15b, K0), *Arthemisia campestris* (K90), *Asperula cynanchica* (K180a, K180b, K60), *Astragalus glyciphyllos* (K15a), *Avenula pratensis* (K180a, K180b, K90, K60, K40, K15a), *Avenula pubescens* (K180a, K180b, K60, K40, K15a), *Brachypodium pinnatum* (K180a, K90, K60, K40), *Briza media* (K180a, K180b, K60, K40), *Bromus commutatus* (K15b), *Bromus erectus* (K180a), *Campanula rapunculoides* (K60, K15a), *Campanula rotundifolia* (K180a, K60, K40), *Carlina acaulis* (K180a), *Centaurea jacea* (K180a, K60, K40), *Centaurea rhenana* (K180a, K180b, K40), *Centaurea scabiosa* (K180b, K40, K15b), *Cerastium arvense* (K180a, K60, K40, K15a, K0), *Cerastium pumilum* agg. (K40), *Cirsium acaule* (K180a, K60, K40), *Cirsium arvense* (K15b), *Convolvulus arvensis* (K180a, K15a, K15b), *Cynoglossum officinale* (K15a), *Dactylis glomerata* (K180a, K90, K60, K40, K15a, K15b), *Daucus carota* (K0), *Dianthus carthusianorum* (K180a, K60, K40), *Echium vulgare* (K40), *Erophila verna* (K40), *Euphorbia cyparissias* (K180b, K40, K15a), *Euphrasia* sp. (K180a), *Falcaria vulgaris* (K90, K15a), *Festuca pratensis* (K40, K15a, K15b), *Festuca rubra* agg. (K40, K15a), *Festuca rupicola* (K180a, K180b, K90, K60, K40, K15a, K15b), *Fragaria viridis* (K90, K40, K15a), *Galium mollugo* s.l. (K60, K40, K15b), *Galium verum* (K15a), *Genista sagittalis* (K180b), *Geranium* cf. *columbinum* (K15a), *Geranium pusillum* (K0), *Helianthemum nummularium* s.l. (K60), *Hieracium pilosella* (K180a, K90, K60, K40), *Hippocrepis comosa* (K180b, K60, K40), *Chamaecytisus ratisbonensis* (K60, K40), *Knautia arvensis* (K180a, K90, K60, K40, K15b), *Koeleria macrantha* (K180a), *Koeleria pyramidata* (K180a, K180b, K90, K40, K15a), *Lathyrus pratensis* (K90, K15a), *Leontodon hispidus* (K60), *Leucanthemum vulgare* (K60), *Ligustrum vulgare* (K180b, K90), *Linaria vulgaris* (K90, K15b), *Linum catharticum* (K40), *Lolium perenne* (K15b), *Lotus corniculatus* (K180a, K180b, K40), *Luzula campestris* (K180b), *Medicago falcata* (K60, K15a), *Medicago lupulina* (K40), *Medicago sativa* (K15b), *Melilotus officinalis* (K15b), *Muscari comosum* (K15a), *Ononis repens* (K60), *Orchis morio* (K180a), *Phleum phleoides* (K180a, K60), *Phleum pratense* (K15a), *Pimpinella saxifraga* (K180a, K180b, K90, K60), *Plantago lanceolata* (K15a), *Plantago media* (K180b), *Poa angustifolia* (K15b), *Polygala comosa* (K180a, K40), *Potentilla* x *subarenaria* (K180b, K40), *Primula veris* (K40), *Prunella grandiflora* (K180a, K180b), *Prunus spinosa* (K180b, K90, K60, K40, K15a, K15b), *Pulsatilla vulgaris* (K180b, K90), *Ranunculus bulbosus* (K180b, K40), *Rosa canina* (K90), *Rumex acetosa* s.l. (K15a), *Salvia pratensis* (K180b, K15a), *Sanguisorba minor* (K180b, K15a, K15b), *Scabiosa columbaria* (K180a), *Secale cereale* (K0), *Securigera varia* (K180a, K60, K40, K15a), *Senecio jacobaea* (K60, K40), *Seseli annuum* (K180b), *Silene latifolia* subsp. *alba* (K60), *Stellaria graminea* (K40), *Taraxacum* sect. *Erythrosperma* (K180a, K60, K15a), *Taraxacum* sect. *Ruderalia* (K180a, K180b, K90, K60, K40, K15a, K15b), *Teucrium chamaedrys* (K180b), *Teucrium montanum* (K180b), *Thlaspi perfoliatum* (K180b), *Thymus praecox* (K180a, K180b, K40), *Thymus pulegioides* (K60, K40), *Tragopogon dubium* (K60, K15b), *Trifolium alpestre* (K180b), *Trifolium dubium* (K40), *Trifolium hybridum* (K15b), *Trifolium medium* (K60), *Trifolium montanum* (K60), *Trifolium pratense* (K40), *Valerianella locusta* (K0), *Veronica arvensis* (K0), *Veronica chamaedrys* (K15a), *Veronica praecox* (K0), *Vicia cracca* agg. (K180a, K90, K60, K15a), *Vicia hirsuta* (K15b), *Vicia sativa* s.l. (K40, K15a), *Viola hirta* (K40).

Appendix 4.4. – List of species present in the vegetation which were not found in the seed bank at individual localities in the Kaltes Feld study region. The species list of aboveground vegetation for each locality resulted from five pooled 2×2 m vegetation plots and was compared with the list of species present in the bank of the given locality. Species are listed in alphabetical order. Additional information regarding the occurrence at individual localities is given in brackets.

Acer campestre - juv. (F180a, F180b, F153, F100, F50b), *Agrimonia eupatoria* (F180a, F180b, F153, F100, F50a, F50b, F8), *Agropyron repens* (F153), *Achillea millefolium* (F180a, F153, F100, F50a, F50b, F8, F0), *Allium oleraceum* (F50b), *Antennaria dioica* (F180b), *Anthyllis vulneraria* (F50a), *Arabis hirsuta* (F180a), *Arrhenatherum elatius* (F153, F50a, F50b), *Aster amellus* (F180a), *Astragalus glycyphyllos* (F50b), *Avena sativa* (F0), *Avenula pratensis* (F180b, F153), *Avenula pubescens* (F153, F100, F8), *Bellis perennis* (F8), *Brachypodium pinnatum* (F153, F100, F50a, F50b), *Briza media* (F180a, F180b, F153, F100), *Bromus erectus* (F180a, F180b, F153, F100, F50a, F50b), *Bupthalmum salicifolium* (F180b, F100, F50b), *Campanula rotundifolia* (F50a), *Carex montana* (F153), *Carlina acaulis* subsp. *caulescens* (F180a, F180b, F153, F100), *Carlina vulgaris* (F180b, F100, F50a, F50b), *Carpinus betulus* - juv. (F180a, F153), *Centaurea jacea* (F180b, F50a, F50b), *Centaurea scabiosa* (F50a), *Cerastium arvense* (F153), *Cerastium holosteoides* (F50a), *Cirsium acaule* (F180a, F180b, F153, F100, F50a, F50b), *Cirsium arvense* (F0), *Cirsium eriophorum* (F153), *Clematis vitalba* (F50a), *Clinopodium vulgare* (F153), *Cornus sanguinea* (F100, F50a, F50b), *Corylus avellana* - juv. (F153), *Cynosurus cristatus* (F153), *Dactylis glomerata* (F180a, F180b, F153, F100, F50a, F50b, F8), *Euphorbia cyparissias* (F180a, F50a), *Euphorbia exigua* (F0), *Euphorbia helioscopia* (F0), *Euphorbia verrucosa* (F180a, F180b), *Euphrasia* sp. (F153), *Fallopia convolvulus* (F0), *Festuca ovina* subsp. *guestfalica* (F180a, F180b, F153, F100, F50b), *Festuca pratensis* (F180b, F153, F100, F50a, F8), *Fragaria vesca* (F153), *Fraxinus excelsior* - juv. (F180a, F153, F100), *Fumaria* cf. *officinalis* (F0), *Galium aparine* (F0), *Galium mollugo* s.l. (F153, F50a, F50b, F8), *Galium verum* (F180b, F153, F50b), *Gentiana cruciata* (F153, F100, F50a), *Gentiana verna* (F180b), *Gentianella ciliata* (F100), *Gentianella germanica* (F180b, F100), *Gymnadenia conopsea* (F180a, F180b, F100, F50a, F50b), *Helianthemum nummularium* s.l. (F180a, F50b), *Hieracium pilosella* (F180b), *Hippocrepis comosa* (F180b), *Hordeum vulgare* (F0), *Juniperus communis* (F180a, F180b), *Knautia arvensis* (F180a, F153, F100, F50a, F50b), *Koeleria pyramidata* (F180a, F180b, F153, F100), *Lapsana communis* (F0), *Lathyrus pratensis* (F153, F50b, F8), *Lathyrus tuberosus* (F0), *Leontodon hispidus* (F180a, F180b, F153, F100, F50b), *Ligustrum vulgare* (F180a, F100, F50a, F50b), *Linaria vulgaris* (F50a), *Lolium perenne* (F0), *Lotus corniculatus* (F8), *Malva* sp. (F0), *Medicago falcata* (F180a, F180b, F100, F50a), *Medicago lupulina* (F0), *Medicago sativa* (F50a, F50b), *Melampyrum arvense* (F50a, F50b), *Melilotus officinalis* (F50a, F50b), *Onobrychis vicifolia* (F100, F50b), *Ononis repens* (F153, F50a, F50b), *Ononis repens* x *spinosa* (F180a, F153, F50a, F50b), *Ononis spinosa* (F180a, F180b, F100), *Papaver dubium* agg. (F0), *Picea abies* - juv. (F50b), *Picris hieracioides* (F50a), *Pimpinella major* (F8), *Pimpinella saxifraga* (F180b, F153, F50a, F50b), *Plantago media* (F180a, F8), *Platanthera bifolia* (F100), *Poa angustifolia* (F8), *Polygala comosa* (F180a, F153), *Potentilla erecta* (F100), *Potentilla neumanniana* (F50a, F50b, F8), *Primulla veris* (F50a), *Prunella vulgaris* (F50a), *Prunus spinosa* (F180a, F153, F100, F50a, F50b), *Quercus robur* -juv. (F100), *Ranunculus acris* (F8), *Ranunculus bulbosus* (F180b), *Rhinanthus alectrolophus* (F153), *Rhinanthus minor* (F180a, F180b, F100, F50b), *Rosa canina* (F180a, F153, F50a), *Rumex acetosa* (F153, F8), *Salvia pratensis* (F50a, F50b), *Salvia verticillata* (F50a), *Sanguisorba minor* (F180b, F8), *Scabiosa columbaria* (F180a, F180b, F50a, F50b), *Sedum acre* (F8), *Senecio erucifolius* (F180b, F50a), *Senecio jacobaea* (F50b), *Silene vulgaris* (F0), *Taraxacum* sect. *Ruderalia* (F180b, F153, F100, F50a, F8), *Thymus pulegioides* subsp. *carniolicus* (F100), *Tragopogon dubium* (F180b, F8), *Trifolium dubium* (F153), *Trifolium medium* (F180a, F50a), *Trifolium pratense* (F180a, F180b, F100, F50a, F50b, F8, F0), *Trisetum flavescens* (F153, F100, F50a, F8), *Triticum* cf. *aestivum* (F0)
Valeriana officinalis s.l. (F50a), *Veronica chamaedrys* (F180a, F50a, F8), *Veronica teucryum* (F50b), *Vicia cracca* (F100, F50a, F50b), *Vicia sativa* s.l. (F8), *Vincetoxicum hirundinaria* (F180a, F100, F50a, F50b), *Viola hirta* (F153, F50a, F50b).

Appendix 4.5. – Values of seed bank density from different grassland types across Europe. Seed bank densities measured in the Kallmünz and Kaltes Feld regions are presented in Fig. 4.3.

Grassland type	Localization and basic geographical description (altitude, annual mean temperature, annual mean precipitation)	Habitat, condition (e.g. degradation)	Seed bank density (seedlings/m^2)	Source
Dry grasslands	Middle Germany, near Halle; 100–160 m, 9.4 °C, 460 mm	dry grassland on volcanic bedrock (*Thymo-Festucetum cinereae*)	mean 2600 (907–5523)	Jackel, 1999
	Middle Germany, Niederklee - southern of Giessen; 230 m, 9.0 °C, 609 mm	ancient dry calcareous grassland (*Gentiano-Koelerietum*)	3332	Fischer, 1987
		recent dry calcareous grassland (*Gentiano-Koelerietum*)	8912	Fischer, 1987
	Czech Republic - Bohemian Karst; 255 m, 8.0–9.0 °C, 480–530 mm	10 years old-field xeric fallow	6875	Soukupová, 1984
		50 years old-field xeric fallow	4063	Soukupová, 1984
		ancient calcareous grassland	1544	Karlík - unpublished data
	northern France - Seine valley near Rouen; 50 m, 11.0 °C, 800 mm	open and grazed dry calcareous grassland	1800–2860	Dutoit and Alard, 1995
		tall grassland	5252	Dutoit and Alard, 1995
	Switzerland, near Schaffhausen; 450 m, 8.5 °C, 883 mm	*Mesobrometum*	3000	Ryser and Gigon, 1985
	southeasternmost part of The Netherlands; 150 m, 11.0 °C, 780 mm	managed calcareous grassland	3500–4000	Willems and Bik, 1998
	Belgium, near Rochefort; 250 m, 11.0 °C, 750 mm	mesophilous calcareous grassland (*Brometalia erecti*)	4645	Bisteau and Mahy, 2005
	central France, near Blois; 90–110 m, 12.4 °C, 635 mm	ancient limestone grassland	3606–6696	Forey and Dutoit, 2012
		recent limestone grassland, approx. 100 years old	2318–6053	Forey and Dutoit, 2012
	north-eastern Hungary, Zemplén Mts.; 640–720 m, 7.5–8.0 °C, 750–800 mm	acidic dry-mesophilous meadow (*Cirsio pannonicae-Brachypodion pinnati*)	4400–6300	Valkó et al., 2011
	Southern Germany, Swabian Alb; 700 m, 6.5 °C, 1114 mm	grazed and mown calcareous grassland (*Gentiano-Koelerietum*, *Mesobrometum*)	6000–7000	Poschlod and Jackel, 1993
	England, Sussex, near Brighton; 160 m, 11.0 °C, 600 mm	chalk grasslands – mesophilous with only few xerotermophilous species, degradated	mean 6770	Graham and Hutchings, 1988
	southwestern Sweden, at Lake Vänern; 150 m, 6.6 °C, 650 mm	limestone grassland (*Veronica spicata-Avenula pratensis* association)	mean 10,060	Milberg and Hansson, 1993
Mesophilous and semi-wet meadows	Germany, Rhine floodplain between Mainz and Mannheim; 85 m, 10.3 °C, 580 mm	hay meadow (*Arrhenatherion*)	4060	Holzel and Otte, 2001
		hay meadow (*Cnidion*)	6860–8680	Holzel and Otte, 2001
	south-western Germany, Mittleren Schwarzwald; 300–620 m, 7.0 – 9.0 °C, 1000 mm	mesophilous meadow (*Arrhenatheretum typicum*)	5319–7017	Kretzschmar, 1992; 1994
	Middle Germany, Lahn-Dill Highlands; 200–600 m, 6–8 °C, 900–1100 mm	mesic grassland (*Arrhenatheretalia*) – hay meadow, pasture	8809–9125	Wellstein et al., 2007
	south-western Germany, Mittleren Schwarzwald; 1110 m, 5.5 °C, 1500 mm	mountain meadow (*Geranio-Trisetetum typicum*)	12,344	Kretzschmar, 1992; 1994
	Czech Republic - Krkonoše Mts.; 590–1265 m., 3.0–5.0 °C, 800–1200 mm	mountain meadow (*Polygono bistortae-Trisetion flavescentis*)	mean 18,108	Handlová and Münzbergová, 2006
	southern Finland; 50 m, 6.0 °C, 625 mm	21 years old-field wet fallow	mean 31,000	Kiirikki 1993

Chapter 5

Soil seed banks and aboveground vegetation of a dry grassland in the Bohemian Karst

Abstract

This paper is the first contribution to knowledge about the soil seed banks of ancient grasslands in the Bohemian Karst (Český kras). This region is highly valuable from the nature conservancy perspective and is famous for its dry grasslands, especially those belonging to the alliance *Festucion valesiacae*. The vegetation of the study site belongs to the alliance *Cirsio-Brachypodion* with a strong dominance of *Bromus erectus*, which suppresses the species diversity of aboveground vegetation. It is probably an alien species in the region. Nevertheless, some rare species, such as *Aster amellus*, *Helianthemum canum*, *Pulsatilla pratensis* and *Stachys germanica*, are also present. The soil seed bank is very small in both species and seedling numbers are low. The absence of weeds and species of young grasslands in the soil seed bank confirms that the site was not used as an arable field in the past. The presence of germinable seeds of *Potentilla incana*, *Linum catharticum*, *Sedum acre* and *S. sexangulare* indicates that the grassland under study was once richer in species thanks to grazing-induced disturbances. The potential of soil seed banks for the restoration of species-impoverished grasslands is discussed.

Key words: Karlštejn Nature Reserve, calcareous grasslands, ancient grasslands, soil seed bank, similarity index, Bohemian Karst/Český kras, restoration ecology

Introduction

Dry grasslands are considered a high-priority biotope from a conservation standpoint because of their high species diversity, which includes a wide range of rare species (e.g. Korneck et al. 1998, Wallis DeVries et al. 2002, Dengler 2005). For this reason, management measures are in place to improve the nature conservancy status of degraded and species-impoverished dry grasslands. Proposed measures include pasturage, transfer of diaspores with hay and similar practices, and the utilization of potential of soil seed banks (Kubíková 1999). The possibility to use soil seed banks to reconstruct past vegetation is based upon the fact that seeds of plants can, under certain conditions, survive in soil for centuries, which is especially true for certain weeds of arable fields (Priestley 1986, Telewski & Zeevaart 2002, Karlík & Poschlod 2014). However, a number of studies have shown that this potential is strongly limited in the case of dry grasslands (e.g. Graham et Hutchings 1988, Willems 1995, 2001; Bakker et al. 1996, Bekker et al. 1997, Poschlod et al. 1998, Mitlacher et al. 2002, Bossuyt & Hermy 2003, Bisteau & Mahy 2005, Valkó et al. 2011). It is generally true that, in a given habitat, the density of soil seed banks in dry grasslands decreases with decreasing climate humidity and with decreasing soil humidity (Karlík & Poschlod 2014). Whereas in dry grasslands of the association Bromion erecti s.l. the density of the seed bank is usually around 3,000–5,000 seeds per m2, in mesophilous oatgrass meadows it is around 5,000–10,000 seeds per m2, and in fenny and other wetland meadows it reaches tens of thousands of seeds per m2, which is to a certain extent given by the presence of a few enormously abundant species, especially rushes. One of the main reasons behind this phenomenon is that typical species of dry grasslands, such as Pulsatilla pratensis, do not produce dormant seeds and therefore germinate soon after seed shed. Such species have only transient seed banks (Thompson et al. 1997). As some arable weeds have become very rare, soil seed banks can be potentially used in the restoration of the weed flora. Their seeds are conserved in the soil of former fields currently overgrown by dry grassland vegetation (Forey & Dutoit 2012, Karlík & Poschlod 2014). Many weeds are known for their long-persistent soil seed banks (Priestley 1986, Bekker et al. 1998) and their occurrence in present-day dry grasslands can be considered an indication of their previous arable use (Fischer 1987, Karlík & Poschlod 2014).

Seed bank research is a specialized branch of vegetation science since the 1950s (e.g. by Bogdanovskaya-Gienef 1954). In this context, the research by Soukupová (1984, 1990) of differently aged abandoned fields in the Bohemian Karst, carried out in the second half of the 1970s, has significantly contributed to knowledge about the importance and dynamics of soil seed banks in grasslands and abandoned fields. The mentioned study was carried out as part of a broadly conceived investigation of succession on abandoned fields in the Bohemian Karst (Osbornová et al. 1990), which was later expanded on by Jírová et al. (2012). The latter study, however, only deals with abandoned fields, and, as far as the author of the present article is aware, no study on the soil seed banks of continuous grasslands (i.e. those continuously utilized as grasslands for at least 170 years) has been carried out in the Bohemian Karst.

The main objectives of the present study were to ascertain the basic characteristics of the soil seed bank at a locality with the continuous occurrence of a dry grassland, to determine its similarity with aboveground vegetation and to evaluate the potential utility of soil seed banks in restoration ecology.

Study site

The study site is part of the Český kras Protected Landscape Area and is located in the southwestern extremity of the Karlštejn National Nature Reserve, south of the village of Srbsko. It is situated at the top of a steep cliff above the river Berounka and is oriented towards the southwest, above the precipice on a gentle slope with an inclination of less than 10° (Fig. 5.1, 5.2).

The geological substrate of the whole study site consists of Early Devonian limestone. Pleistocene gravel-sand terraces are present directly above the study site to the north and east, in the area of an abandoned field. The soil at the site is of the rendzina type. The average annual temperatures in the area are 8–9°C and the annual average precipitation sums are 480–530 mm (Ložek et al. 2005).

On old maps from the year 1840, the site is marked as part of a communal pasture, so it can be considered an ancient (continuous) grassland (Poschlod et al. 2008, Karlík & Poschlod 2009). As to when pasturage (or mowing) ceased at the site is not exactly known. In any case, in the last few decades, the site has not been managed in any way.

To the south and west of the site there are rock steppes on a steep slope above the river Berounka. To the east of the site are vast expanses of abandoned fields.

From a vegetational perspective, the site is overgrown by vegetation of the association *Cirsio-Brachypodion pinnati* with elements of the association *Festucion valesiacae*. They are species-depauperate stands with a strong dominance of *Bromus erectus*. Such stands are typical for the

Bohemian Karst, especially in the vicinity of villages, and stand in contrast with well-developed and floristically highly diverse communities of the association *Festucion valesiacae*, which are found on rock steppes further away from human settlements.

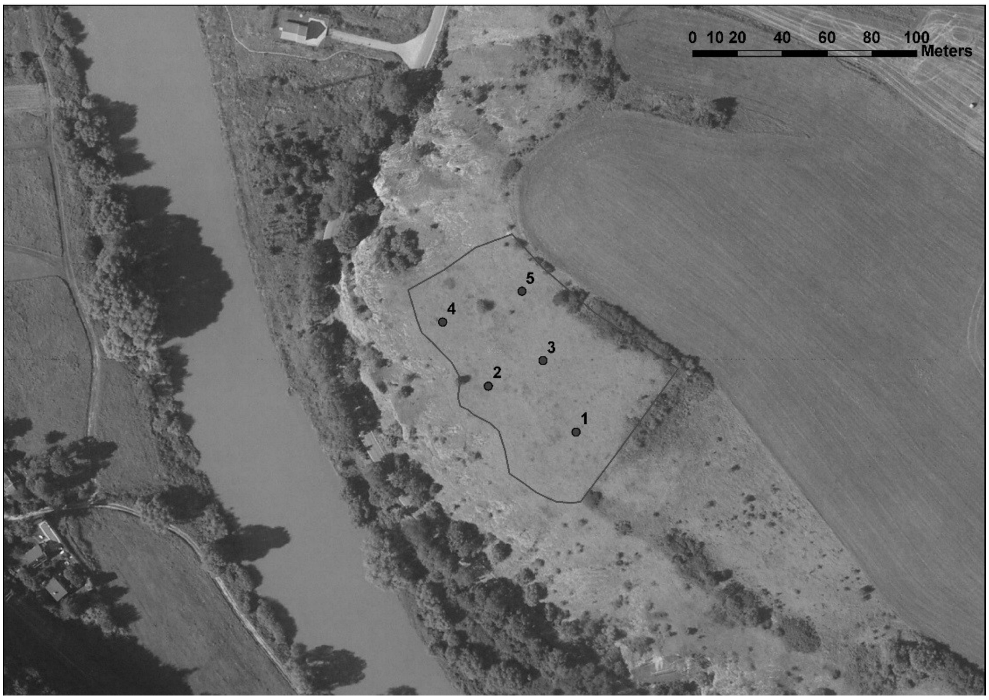

Fig. 5.1. – Locations of sample plots No. 1–5 within the study site (geographical basis: CENIA).

Methods

Five quadrats were placed so as to represent the vegetation of the locality, disregarding rocky outcrops and shrubby vegetation. Soil samples for seed bank analysis were taken on 9 March 2007 (Fig. 5.1). The composition of the current vegetation of vascular plants in these plots was recorded on 7 August 2008 using the phytosociological relevé method in 2×2-m quadrats. The Braun-Blanquet nine-degree abundance-dominance scale was used (Barkman et al. 1964). Also recorded was the vegetation of the moss layer. Selected herbarium specimens were identified by bryologist Jiří Váňa and lichenologist Jiří Malíček.

Also recorded were environmental variables such as the inclination and orientation of the slope, the dominance of different vegetation layers and soil depth (ascertained as the average of eight soil depth measurements obtained by sticking a 6-mm diameter wire into the soil).

The composition of the seed bank was ascertained by a method based on the identification of emerged seedlings (ter Heerdt et al. 1996). Soil samples were collected in early spring after the stratification of seeds over. The sampling was performed using a steel pedological auger with a diameter of 40 mm, yielding 10 cm long cylindrical soil monoliths. Each monolith was halved and the resulting samples (i.e. the upper and lower layer) were further processed separately. Ten such such monoliths were sampled in each plot. Thus, at each plot, 126 cm2 of soil was. The samples were transported in plastic bags to the laboratory, where they were stored at 4°C until the end of March, when they were cultivated. To ensure the emergence of the maximum number of seeds, the volume of each sample was reduced (ter Heerdt et al. 1996). The soil was rinsed with water on a sieve with a mesh opening size of 0.2 mm. Reduced soil samples containing seeds were transferred to a cultivation dish filled with a sterilized garden substrate and spread into an approximately 3-mm layer. For the purpose of detecting possible contamination of samples by seeds not initially present in the seed bank, control dishes containing only the garden substrate without the addition of a soil sample were placed among the sample dishes. These controls allowed to exclude contamination by taxa with seeds dispersed by wind or active ejection (*Betula* spec., *Salix* spec., *Epilobium* spec., *Taraxacum* sect. *Ruderalia* and *Cardamine hirsuta*), whose occurrence was not taken into account in the data evaluation.

The samples were cultivated for 14 months (i.e. until new seedlings stopped emerging) in an unheated greenhouse. Identified plants were removed from the dishes in the seedling stage. Seedlings that could not be identified were replanted in a separate pot and cultivated until the plants could be identified. Two seedlings were not identified because they perished before they could be determined.

The Sørensen index of similarity was used to ascertain the floristic similarity between the seed bank and aboveground vegetation (Sørensen 1948, Hopfensperger 2007). It is calculated as 2C/(A+B), where 'C' is the number of species shared by the aboveground vegetation and the seed bank, 'A' is the number of species present in the vegetation, and 'B' is the number of species present in the seed bank.

The botanical nomenclature follows Rothmaler (2005), Frahm and Frey (2004), and Wirth (1995). Red-listed species of vascular plants encountered (Grulich 2012) fall into the following categories: strongly threatened species (category C2), threatened species (category C3) and species requiring attention (category C4a). Names of syntaxa are unified in accordance with the newly published compendium The Vegetation of the Czech Republic (Chytrý 2007), where broadleaf dry grasslands are divided into two associations: *Cirsio-Brachypodion pinnati* and *Bromion erecti* (sensu stricto). When talking about these grasslands in a general sense without the possibility or intent to differentiate them further, the older concept of this vegetation is used, which is referred to in the text below as *Bromion erecti* sensu lato (Moravec 1995).

Results

<u>Soil seed bank</u>

Altogether, the cultivation yielded 97 seedlings, which corresponds to a density of 1,363 seedlings per m^2. The seedlings were determined to belong to 17 species of vascular plants (Table 5.1). It is possible that the anemochorous species *Conysa canadensis* and *Sonchus arvensis* got into the greenhouse as contamination; however, they were not recorded in any of the control dishes.

The most frequent species present in the seed bank was *Hypericum perforatum* followed, at considerable distance, by *Linum catharticum*. Recorded in smaller numbers were a few species typical of dry grasslands and also some weeds. The floristically and conservationally most striking was the species *Helianthemum canum* (C2). This phytogeographically significant species occurs in the Czech Republic, besides steppes of the Bohemian Karst, only on grassy hillsides known as 'bílé stráně' (meaning 'white hillsides') near the towns of Roudnice nad Labem and Štětí (Hrouda 1990, Florabase 2013). Also of significance is the finding of *Arabis sagittata* (C3), whose ability to establish a longer-term seed bank had not been known (LEDA 2013). More seeds were contained in the upper soil layer than in the lower one.

Table 5.1. – Numbers of seedlings emerged from soil seed bank samples from five sample plots. Upper ('h') and lower ('d') soil layers are differentiated. The presence of particular species in both the seed bank and in aboveground vegetation is indicated by italicized numbers of seedlings on a grey background.

	1	1h	1d	2	2h	2d	3	3h	3d	4	4h	4d	5	5h	5d
Amaranthus retroflexus													**4**	4	
Arabis hirsuta agg. *)	**1**	1								***2***	*1*	*1*			
Arenaria serpyllifolia	**1**	1		**2**		2							**2**	2	
Cerastium holosteoides							**2**	2							
Conyza canadensis				**1**	1		**1**		1						
Galinsoga ciliata	**1**	1		**1**		1									
Helianthemum canum							***1***	*1*					**1**	1	
Hypericum perforatum	**30**	13	17	**12**	10	2	***1***	*1*					***2***	*2*	
Linum catharticum				**3**	1	2				***5***	*4*	*1*	**3**	3	
Medicago lupulina													**1**		1
Poa pratensis s.l.	**1**		1	**1**	1		**1**		1				**1**	1	
Potentilla cinerea	**1**		1				***1***	*1*		**1**		1			
Sedum acre	**1**	1													
Sedum sexangulare				**1**		1							**1**		1
Sonchus arvensis				**2**	1	1				**1**	1		**1**	1	
Teucrium chamaedrys				***1***	*1*										
Verbascum lychnitis	**2**	1	1										**1**	1	
Not identified										**1**	1		**1**	1	
Number of species	**8**	6	4	**9**	6	6	**6**	4	2	**4**	3	3	**10**	8	2
Number of seedlings	**38**	18	20	**24**	15	9	**7**	5	2	**10**	7	3	**18**	16	2

*) Both species of the collective taxon *Arabis hirsuta* agg. occur at the site. Cultivated from sample 4 were plants that were reliably identified as *Arabis sagittata*.

<u>*Vegetation*</u>

In the past, the locality served as a pasture. However, this has been abandoned for several decades. Still, however, there is a relatively highly stabilized dry grassland community that is resilient against the establishment of woody species, which would lead to succession into a shrubland and, eventually, a woodland. The grassland consists of monodominant stands of *Bromus erectus*, which are at first sight not too rich in species because of the strong dominance of brome.

As concerns its phytosociological classification, the vegetation under study belongs to the class *Festuco-Brometea*. Syntaxonomically, they are not too characteristic stands of the alliance *Cirsio-Brachypodion pinnati*, association *Scabioso ochroleucae-Brachypodietum pinnati* (sensu Chytrý 2007), and there is a conspicuous transition towards vegetation of the association *Festucion valesiacae*, especially in places with shallower soil (see relevé 3; abundant *Teucryum chamaedrys*, *Helianthemum canum* and also, for example, *Potentilla cinerea*).

The vegetation of the study plots is summarized in Table 5.2. The five phytosociological relevés comprise a total of 33 species of vascular plants. Further 18 species were recorded outside of the relevés: *Aster amellus* (C3), *Anthyllis vulneraria*, *Asperula cynanchica*, *Carduus nutans*, *Carlina vulgaris*, *Centaurea rhenana*, *Echium vulgare*, *Inula hirta* (C3), *Lactuca serriola*, *Poa angustifolia*, *Pulsatilla pratensis* (C2), *Salvia pratensis*, *Scabiosa ochroleuca*, *Seseli osseum* (C4a), *Stachys germanica* (C2), *Stachys recta*, *Verbascum lychnitis* and *Vincetoxicum hirundinaria*.

Along the perimeter of the site, and to a lesser degree also within it, there are spontaneously growing trees and shrubs, namely *Carpinus betulus*, *Crataegus* sp., *Cerasus avium*, *Fraxinus excelsior*, *Prunus spinosa* and *Quercus robur*.

Altogether 15 currently red-listed species of vascular plants were found at the site (Grulich 2012; Table 5.2).

Table 5.2. – Table of vegetation plots (phytosociological relevés). All relevés (2×2 m quadrats) were recorded on August 7 2008. In the first column, categories of endangerment according to the Czech Red List (Grulich 2012) are given.

	Relevé number	**1**	**2**	**3**	**4**	**5**
	Orientation (°)	225	225	225	225	225
	Slope (°)	7	5	6	5	7
	Latitude (WGS84)	495556,	495556,	495557,	495557,	495557,
	Longitude (WGS84)	140815,	140812,	140813,	140810,	140812,
	Herb layer (%)	75	75	70	72	72
	Moss layer (%)	15	15	20	10	15
	Stones (%)	1	0	1	0	0
	Soil depth – Mean	10,50	10,88	7,50	12,00	10,13
	Number of species	9	10	15	17	19
	Herb layer					
	alliance *Bromion erecti* s.l.					
	Bromus erectus	4	3	3	2b	3
	Securigera varia	1		+	2a	+
	Pimpinella saxifraga	r	r	+	+	r
	Centaurea scabiosa		r			2a
C4	*Cirsum acaule*				1	1
	Sanguisorba minor				r	r
	Fragaria viridis				+	+
	Helianthemum nummularium		+		1	
	Brachypodium pinnatum		1			
	Centaurea jacea					+
	Galium verum					+
C3	*Thesium linophyllon*				+	
	Linum catharticum				+	
	alliance *Festucion valesiacae*					
C4	*Teucrium chamaedrys*	+	2a	2b	+	+
C2	*Helianthemum canum*			2b	+	
	Festuca valesiaca	1	+			
	Koeleria macrantha	1				r
C3	*Seseli hippomarathrum*	+		+		
	Dianthus carthusianorum			r		r
	Eryngium campestre	1				
C4	*Potentilla cinerea*			1		
	Sesleria albicans				2a	
	class *Festuco-Brometea* and other					
C4	*Carex humilis*		2a	2b	2b	2a
	Festuca rupicola	+	+	+	+	+
(C3	*Arabis hirsuta* agg.		r	r	+	
C4	*Thymus praecox*			+		+
	Achillea collina			+		+
	Hypericum perforatum			r		+
	Euphorbia cyparissias			r		
	Asperula tinctoria				+	
C4	*Anthericum ramosum*				r	
	Campanula rotundifolia					r
	Inula conyzae					r
	Moss layer					
	Abietinella abietina	2b	+	+	1	2a
	Fissidens taxifolius	+		1	1	+
	Cladonia rangiformis	+	+	2a		
	Bryum capillare			1		+
	Weissia controversa			1		+
	Cladonia furcata				+	1
	Hypnum lacunosum				1	+
	Rhytidium rugosum		2a		1	
	Homalothecium lutescens		1			
	Cladonia pocillum			1		
	Entodon concinnus					+

Note concerning *Arabis hirsuta* agg.: The threatened species *Arabis sagittata* (C3) prevails at the site (and occurs, among others, in relevés 2 and 4). However, *A. hirsuta* s. str. without doubt occurs at the site, too.

Comparison of the soil seed bank with aboveground vegetation

Eight taxa were present both in the seed bank and in the vegetation (based on five phytosociological relevés and a list of species growing in their close vicinity): *Arabis hirsuta* agg., *Helianthemum canum*, *Hypericum perforatum*, *Linum catharticum*, *Poa pratensis* s.l., *Potentilla cinerea*, *Teucrium chamaedrys* and *Verbascum lychnitis*.

Similarity between the soil seed bank and aboveground vegetation is expressed as the Sørensen index (Table 5.3).

Table 5.3. – Similarity between the soil seed bank and vegetation calculated using Sørensen's index.

Plot	C (number of species present in the vegetation and the seed bank)	A (number of species present in the vegetation)	B (number of species present in the seed bank)	SI = 2C/(A+B)
1	0	9	8	**0,00**
2	1	10	9	**0,11**
3	3	15	6	**0,29**
4	2	17	4	**0,19**
5	1	19	10	**0,07**

Fig. 5.2. – View to the southwest across the valley of the river Berounka in the direction of the Koda ravine.

Discussion

Soil seed bank

The density of the seed bank turned out to be very low – 1,363 seedlings/m^2. This is very few even compared to data on dry grasslands in Central and Northwest Europe. Similar values were ascertained for continuous grasslands in central Germany near the city of Halle (Jackel 1999) and in southern Germany by the town of Kallmünz (Karlík & Poschlod 2014), which is related to the fact that these two regions have a similar continentally influenced climate with somewhat high mean annual temperatures but very low precipitation sums. Moreover, the number of species represented in the seed bank were relatively low, which can be explained mainly as a consequence of low seed density combined with the small volume of samples and a low number of repeats.

Weedy species were represented in the seed bank only to a small extent. Importantly, species such as *Anagallis arvensis*, *Chenopodium album* agg., *Convolvulus arvensis*, *Veronica arvensis* and *Viola arvenis*, the best indicators of former fields, were entirely absent. Many of them persist in the seed bank for a very long time, even for longer than 150 years (Karlík & Poschlod 2014). In the seedbank of nearby abandoned fields, these species are present (Soukupová 1984, 1990). The emergence of a few of the weed species in the cultivation experiment can therefore be explained mainly by secondary spread (by water runoff) from a field situated higher up the slope (which is obviously the case of *Amaranthus retroflexus* in relevé No. 5), or by contamination of the samples in the greenhouse.

The unabundant presence of weed species, documented above, supports the hypothesis that the site under study was never tilled.

Vegetation

Even though a relatively large number of endangered plant species has been recorded at the site, the vegetation is species-impoverished as a result of a long-term lack of management and a strong dominance of *Bromus erectus.* Phytosociological relevés (4 m^2 in area) captured only 9–19 species of plants (cf. Kubíková 2007, Karlík & Malíček 2008, Poschlod et al. 2008, Karlík & Poschlod 2009). However, despite the obvious impoverishment and a certain degree of degradation, it is obvious, based on the composition of the current vegetation, that the site was not tilled in the past. There are no indicators of young grasslands, although one of the best, *Agrimonia eupatoria* (cf. Poschlod et al. 2008, Karlík & Poschlod 2009), occurs right in the adjacent fallow to the southeast of the study site.

Whereas stands of the association *Festucion valesiacae* in the Bohemian Karst are of excellent quality, stands belonging to the association *Bromion erecti* s.l. are often depauperate, as is the case of the study site. Such impoverished communities are distributed especially in the vicinity of villages and are characterized by a strong monodominance of *Bromus erectus*. The question thus arises whether the abundant distribution of *Bromus erectus* in these grasslands is natural. Its presence might be a result of deliberate introduction with the aim to improve the nutritional quality of the grassland or to support its soil protection function. Alternatively or in addition, brome could have expanded after the cessation of management. The use of *Bromus erectus* for establishing grasslands in Austro-Hungarian Empire and in France is described, for example, by Stiný (1908) or Hard (1964), so it was probably sown also in the Bohemian Karst.

Another question is to what degree, if at all, is *Bromus erectus* a native species, not only in the Bohemian Karst, but also in other regions of the Czech Republic. The map of the species' distribution in Czechia shows a conspicuous concentration of localities in the central part of the Bohemian thermophytic region (especially in the Central Bohemian Uplands and the Lower Vltava region) and also in the Pannonian thermophytic region in southern Moravia (Florabase 2013). Elsewhere, even on potentially suitable geological substrates, it tends to be rare and is clearly associated with secondary habitats (e.g. along railway tracks) or with less preserved dry grasslands (e.g. Karlík & Malíček 2008), which might indicate that *Bromus erectus* is a non-native species that was introduced to the region only in the past few centuries. The character of the distribution of *Bromus erectus* in neighbouring Germany is described by Gauckler (1938), who mentions its gradual disappearance towards the north and explicitly casts doubt on its nativeness in the northern part of the Franconian Jura, which is the geographically closest large limestone region to the Bohemian Karst. Another clue supporting the neophytic nature of *Bromus erectus* is its complete absence from the archaeobotanical macroremains record in the Czech Republic (Petr Kočár, Adéla Pokorná – personal communication; Pokorná et al. 2011).

Comparison of the soil seed bank and aboveground vegetation

The similarity between the vegetation and the seed bank, expressed as the Sørensen index of similarity (Table 5.3), is very low (0–0.29). However, in continuous dry grasslands in southern Germany, where the exact same method was applied, this index most frequently reached values of around 0.3–0.4 (Karlík & Poschlod 2014). Low values were also recorded in ancient fallows of the Podyjí National Park by Entová (2013), who found values in the range of 0.23–0.27. The main reason behind the low similarity is that the seed bank at the study locality is rather poor (see above). It is also, to a certain extent, possible that the vegetation in its current state differs from that recorded by the seed bank as a result of degradation. It seems that the seed bank at the site under study is a reflection of a time when the vegetation was richer in species and with a greater degree of disturbance, possibly as a result of pasturage. This might be indicated by the occurrence of stonecrops (*Sedum* sp. div.), which do not occur in the current vegetation of the plots or in their close vicinity at all. Analogously, the species *Potentilla incana* and *Linum catharticum* are common in the seed bank but occur in the current vegetation only rarely. Lastly, *Poa pratensis* s.l., which is especially abundant in disturbed dry grasslands, is present in the seed bank but not in the current vegetation.

Importance of dry grassland soil seed banks for nature protection

The seed bank at the study site is poor as to the overall number of seeds and the number of species. The only conservationally more important species found in the seed bank were *Arabis sagittata* and *Helianthemum canum*.

Both from a floristic perspective and from the standpoint of plant community restoration, it can be summarized that soil seed banks in continuous grasslands are of limited significance. This result confirms the conclusions reached by studies carried out in other regions, which are outlined in the Introduction. However, this conclusion only pertains to continuous grasslands. The importance of seed banks in young dry grasslands for the preservation of the gene pools of rare weeds of arable fields has been examined by Forey and Dutoit (2012) in central France, by Karlík and Poschlod (2014) in southern Germany, and most recently by Entová in the in southern Moravia (2013).

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Chapter 6

Perspectives of using knowledge about the history of grasslands in nature conservation and restoration practice

In this chapter I deal with the possibilities to use the findings for nature conservation purposes. It is assessed whether and how the history of the sites affects their current conservation status. If so, it is beneficial to try to get to know their history and thus to better understand the subject of protection, the causes of degradation and the possibility of restoration. We can use a variety of aspects during the conservation status assessment. These are discussed in the paragraphs below.

Species richness

Species richness is generally recognized as one way to assess the conservation value of natural or semi-natural ecosystems (e.g. Tilman & Downing 1994). In the case of natural and semi-natural habitats of the same unit (e.g. habitat type or alliance), the number of species usually shows well-preserved state, respectively degradation (Lustyk 2015). The frequency of occurrence of certain indicator species is used practically even when expressing the economic value of nature (HMUKLV 1992, Seják & Dejmal 2003).

Both ancient and recent grasslands in both South German study regions (chapters 2 and 3) are extraordinary species rich. In the Kaltes Feld region, there was no significant difference in the number of species among the grasslands of various age. On average, the richest were 150 years old recent grasslands on the plateau (mean species number 40.6 of vascular plants in 4m^2 plots), and the least rich were ancient grasslands (37.5). However, with regard to absolute values, the highest number of species was recorded in an ancient grassland (56 species). The second highest number of 51 species was recorded in a young grassland (established after 1953). In the Kallmünz region numbers of species in 4m^2 plots were lower. The average number of species per plot tended to be generally higher in ancient grasslands (33.8 species), but significantly lower is only species number in old recent grasslands; see Fig. 3.3 and Table 3.3). The greatest number of vascular plant species was 46 within a 4-m2 plot in a 60 years old recent grassland. Analysis of the Shannon-Wiener Index of diversity leads to a similar conclusion in both regions.

These results do not correspond to other studies that generally indicate higher species richness in ancient grasslands (Ejrnæs & Bruun 1995, Waldhardt & Otte 2003, Waesch & Becker 2009, Forey & Dutoit 2012). The reason may be that the two researched South German regions are well-preserved and grazed by migrating shepherds, across most of their area, and that therefore, young grasslands are well connected to ancient ones.

If we compare the average species richness of sampled plots with regional studies carried out in different regions of Germany (e.g. Rost 1996, Becker 1999, Kiehl & Jeschke 2005, Becker et al. 2012; unfortunately, the synthesis of values for Germany is still lacking), the above-average richness of plots in both studied regions is obvious. For comparison, the Czech vegetation overview (Chytrý 2007) shows the most frequent values of 25-40 species on an area of 16-25 m^2 for semi-dry calacareous grasslands (as. *Gentiano-Koelerietum pyramidatae*, syn. as. *Carlino acaulis-Brometum erecti*).

Although the observed maximal numbers of species in vegetation plot (i.e. 56 species in Kaltes Feld and 46 spacies in Kallmünz) can not be compared to the world records for the semi dry grasslands recorded in the Carpathian region (especially in the White Carpathians, where up to 100 species were found on $4m^2$ scala (Klimeš et al. 2001)), they are above average and are nearing the maxima from other regions (Wilson et al. 2012, Roleček et al. 2014, Chytrý et al. 2015). For example, the Slovak record outside the White Carpathians and Kopanecké lúky is 64 species in 4 m^2 plot from the mesic oligotrophic pasture (*Festuco rupicolae-Nardetum strictae*)(Chytrý et al. 2015).

Another way to compare the species richness of ancient and recent grasslands is to calculate their share of the total species pool of grasslands in the region. Adding all the species of vascular plants (including trees and shrubs) from all the relevés in the region, we obtain 173 species in Kallmünz and 162 species in Kaltes Feld. For completeness, I note that 12 ancient and 11 recent grasslands were included under study in Kallmünz and 10 ancient and 12 recent grasslands were studied in the Kaltes Feld region. In both studies the recent grasslands share obviously more species of the total species-pool. In Kallmünz the recent grasslands hold 84% of the entire species list while ancient grasslands contain only 69% of species (Table 3.2). In Kaltes Feld region in recent grasslands even 92% of all species recorded in the study are found while ancient grasslands accommodate 69% of entire the species list. The explanation is the overall greater diversity of young grasslands (e.g. nutrient content) and the diversity of succession stages. This is related to the fact that, in addition to calcareous grasslands specialists, adapted to nutrient poor conditions and lack of moisture, in young grasslands additionally a number of mesophilous or weedy species grow.

Number of rare and endangered species

An even better indicator of conservation value than a simple number of species is information on the occurrence of endangered species. These species are, of course, preferentially recorded in various conservation mappings, such as habitat mapping for Natura 2000 needs.

In Kallmünz region, 36 % of all recorded species are valuable from a conservation point of view. That means 58 species in all 115 relevés are included in the red-list or protected by law (Table 3.2). More endangered species occur in ancient grasslands (*Anthericum ramosum*, *Chamaecytisus ratisbonensis*, *Genista sagittalis*, *Globularia bisnagarica*, *Hippocrepis comosa*, *Orchis morio*, *Prunella grandiflora* and *Pulsatilla vulgaris*), but many rare species are also typical of recent grasslands (e.g. *Melampyrum arvense*, *Petrorhagia prolifera*, *Polygala comosa* and *Silene otites*) (Appendix 3.1).

Also in the Kaltes Feld region, more endangered species are bound to ancient grasslands (*Antennaria dioica*, *Aster amellus*, *Coeloglossum viride*, *Gentiana verna*). Other species, such as *Gentianella germanica* and *Gymnadenia conopsea*, however, often grow not only in ancient but also recent grasslands. The endangered hemiparasite *Melampyrum arvense* is even an exclusive species of recent grasslands.

The evaluation of the quality of grasslands provided in the text above is based on intensive research, using vegetation relevés or floristic inventories. Another approach to find differences between ancient and recent grasslands, which includes not only selected sites but a more coherent landscape, is extensive mapping of a selected particular species. In the region of Kallmünz I surveyed rare gentian species, which are relevant for nature conservation, and then I analysed if they grow on ancient or recent patches (Poschlod et al. 2008, 2009).

The map in Fig. 6.1 clearly shows that gentians (*Gentiana cruciata*, *Gentianopsis ciliata* and *Gentianella germanica*) are bound to areas of recent grasslands, respectively to former fields and on places with a higher degree of disturbance, such as field boundaries and road margins. The question is whether this has always been the case. It seems that about 160-70 years ago the distribution of gentians was different. There were practically no fallow areas at that time, and the (ancient) dry grasslands were grazed much more intensively (Fig. 1.5 and 1.6). In addition there were many grassland-like field boundaries which were not overgrown by shrubs. There were enough "gaps" in the landscape that ensured the establishment and regeneration of gentian populations from seeds, and that communicated with each other population in terms of metapopulation dynamics (e.g. Eriksson 1996, Johst et al., 2002, Münzbergová & Herben 2004). If we want to support gentian populations, then we have, in my opinion, two major options. Either by higher grazing intensity (smaller cattle breeds are also eligible) or / and by creating artificially disturbed areas. For example, parts of the recent grasslands (former fields) can be tilled at certain intervals (ideally, we will achieve a shiffting mosaik), so that younger succession stages of grasslands are available and the gentians can effectively reproduce by seeds. This method would also be welcome at the same time for the protection of rare weeds.

The low management intensity compared to the past, including protected areas, may be one of the reasons why some rare species are constantly dwindling. Low management intensity leads to increased herb layer coverage, increased biomass and to litter acumulation. Another structure of the grasslands is evident from old vegetation relevés (typically, Gauckler 1938), in which the apparently lower coverage show especially *Bromus erectus* and *Brachypodium pinnatum*, possibly also *Carex humilis* (Quinger et al. 1994).

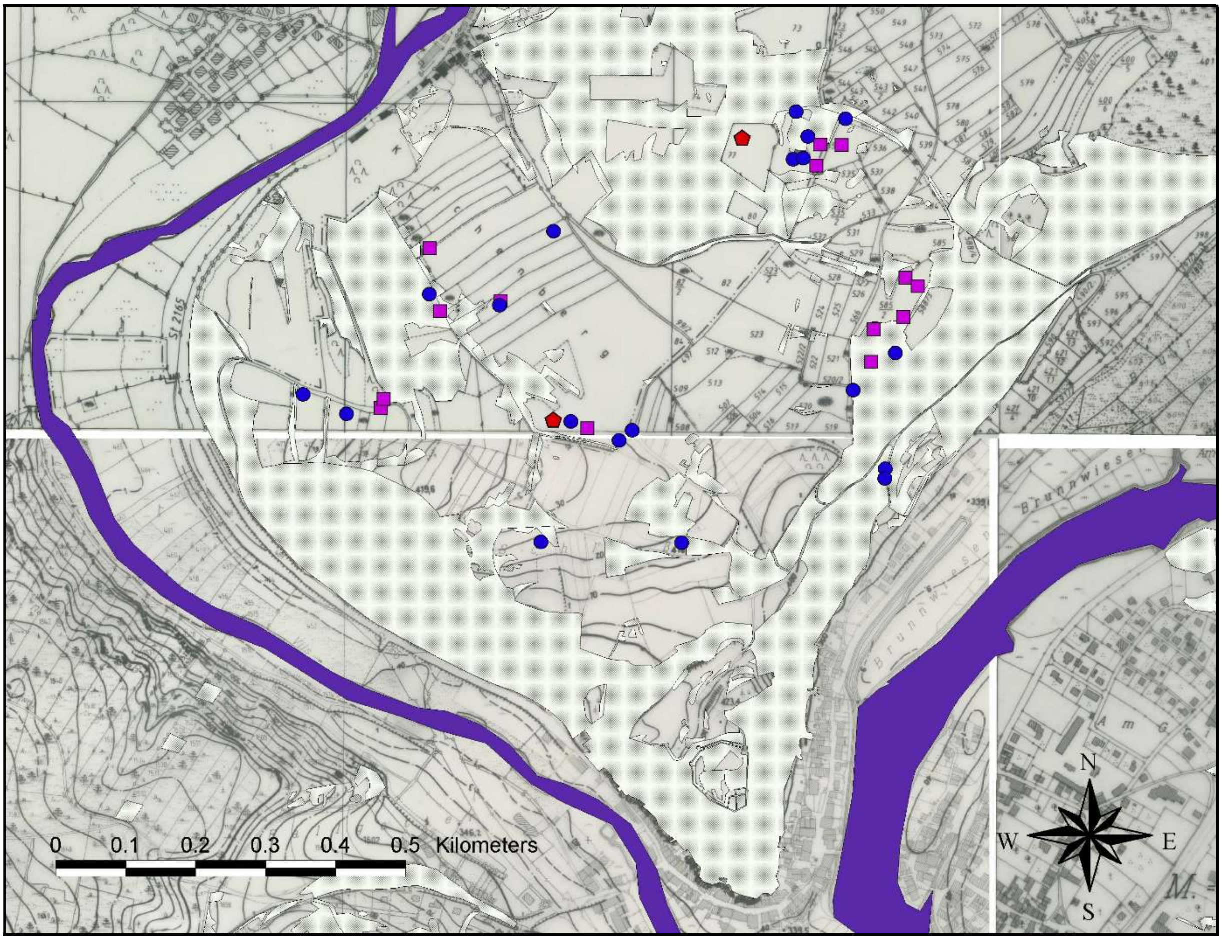

Fig. 6.1. – Occurrence of *Gentiana cruciata* (circles), *Gentianopsis ciliata* (squares) and *Gentianella germanica* (pentagons) on the Schlossberg near Kallmünz. The dotted area indicates the distribution of ancient grasslands. All three gentian species prefer recent grasslands or disturbed habitats like old field borders and pathways. Most data were collected by Petr Karlík; some data about *Gentiana cruciata* were provided by Matthias Dolek.

<u>*Community diversity*</u>

In both regions, ancient grassland species could be clearly assigned to class *Festuco-Brometea* (Oberdorfer 2001, Chytrý & Tichý 2003), whereas recent grasslands tend to be assigned to different phytosociological classes, namely *Festuco-Brometea* and *Molinio-Arrhenatheretea*, but also *Trifolio-Geranietea sanguinei* or *Secalietea cerealis* (Appendix 2.1, Appendix 3.1, Table 3.2).

Some of *Festuco-Brometea* species grow only in ancient grasslands, others are generally distributed (Appendix 1). *Molinio-Arrhenatheretea* species grow with higher frequency and higher cover in recent grasslands. In recent grasslands occur arable weed species, such as *Convolvulus arvensis*, *Cerastium arvense* and the hemiparasitic species *Melampyrum arvense* and *Rhinanthus alectorolophus*.

In recent grasslands some formerly cultivated plants (*Dactylis glomerata*, *Medicago sativa*, *Melilotus officinalis*, *Onobrychis viciifolia*) persist. The above named species are rather common.There are however also some quite rare species (recorded in few or only one plots) restricted to recent grasslands. Examplaes are *Muscari comosum* and *Petrorhagia prolifera* in Kallmünz region and *Thymus pulegioides* subsp. *carniolicus* and *Stachys alpina* in Kaltes Feld. Contrary to the commonly held opinion that more recent habitats have little or no nature conservation value (Waesch

& Becker 2009) we see their importance for a certain part of the regional species pool because these species have often no alternative habitats of occurence.

Another view is that young grasslands represent a specific habitat type. They are, in addition, the current analogy of a very specific habitat, a product of the archaic type of alternate arable field-grassland farming, which is called „wilde Feldgraswirtschaft“ or „Feld-Weidewechselwirtschaft" in German, and which was commonly spread in the Swabian Jurassic mountains until the 19th century (Gradmann 1950). This habitat is also documented in the Kaltes Feld region (Halder 1991, Mailänder 2004). Poschlod &WallisDeVries (2002) state the following species as characteristic for this habitat type: *Ajuga chamaepitys*, *Althaea hirsuta*, *Melampyrum arvense*, *Muscari comosum*, *Onobrychis viciifolia*, *Stachys annua*. Some of these species occur also in the examined regions directly in phytosociological relevés, in marginal parts of grasslands (on old field boundaries) and / or in seed banks.

Relevance of the soil seed bank for the restoration of species diversity and the protection of rare species

The low importance of dry grassland soil seed banks for habitat restoration and their low ability to buffer the extinction of rare species was already described by Poschlod et al. (1998), documented by Stöcklin and Fischer (1999) and newly confirmed by Török et al. (2017). The reasons are very low density of the seed banks, relatively low number of species in the seed banks and with this connected low similarity between the species composition of vegetation and seed banks. These statements I ascertained in all three regions studied (chapters 4 and 5).

The size of the seed bank is generally small compared to other habitats and positively depends on the humidity of the region. In the Kaltes Feld area, with an annual rainfall of 1050 mm, 5457 seedlings/m^2 were cultivated in grasslands of all ages (in ancient grasslands in average 6430 seedlings/m^2 was found). In Kallmünz region, with an annual rainfall of 650 mm, in average 2523 seedlings/m^2 in the differently aged grasslands (1385 seedlings/m^2 in ancient grasslands) were found. In the Bohemian Karst region near Srbsko, with approximatly 500 mm of annual precipitations, only 1544 seedlings/m^2 in an ancient grassland emerged. The both latter regions (Kallmünz and Srbsko) are determinated by dry subcontinental climate. These low values from both regions are comparable with surroundings of Halle in Central Germany, with mean annual precipitations only of 460 mm, where seed-bank density of 2600 seedlings/m^2 is reported (Jackel 1999, Appendix 4.5).

However, this low importance for nature conservation is only true for ancient grasslands. The soil seed bank of recent grasslands may have a high relevance for the conservation of rare weeds. In the seed banks of the study regions I found e.g. *Kickxia spuria*, *Silene noctiflora* and *Stachys annua*; the species which are here extinct from aboveground vegetation. The importance of the soil seed bank of recent grasslands for seed storage of rare arable weeds such as *Althaea hirsuta* was recently also recognized by Forey and Dutoit (2012). Populations of these species are still declining despite many conservation management programmes aimed at their preservation, for example, by leaving stripes along field edges where no fertilizers and herbicides are applied (Otte et al., 1988, 2006). Highly intensive farming in the last decades has even caused these species to disappear from the seed banks of arable fields (Schneider et al., 1994; Schumacher and Schick, 1998). The stock of seeds of these species in the soil of young grasslands therefore provides a significant chance for their restoration.

Although their seed banks gradually diminishes over time, I found germinating seeds of weedy species even in 150 year-old young grasslands.

Therefore, ploughing of appropriately selected recent grasslands without the use of subsequent agricultural techniques such as herbicide application may be an appropriate management method for the re-establishment and maintenance of rare weedy species by activating and refreshing the seed bank. Ploughing of recent grasslands may be a good management tool not only for restoring endangered weed communities but also for helping dry grasslands themselves. Ploughing creates younger successional stages of grasslands, which host disturbance dependent threatened species such as *Gentiana cruciata*. Such actions must be well reasoned and documented, of course.

The presence of weeds in the seed bank of grassland has one more point of view. We can use them to ascertain, respectively verify the history of a particular grassland. The best indicators of former arable field uses are *Anagallis arvensis*, *Chenopodium album* agg., *Convolvulus arvensis*, *Veronica arvensis* and *Viola arvenis*. On the contrary, absence of these species indicate the existence of ancient grasslands (chapter 5).

Age of grasslands and ecological services

Ancient grasslands are generally more important for water retention and carbon sequestration because of higher soil organic matter content and related higher water holding capacity (chapter 3). However, with the setting of specific geological and geomorphological conditions, ancient grasslands can have a very low humus content (chapter 2).

Another ecological service is that recent grasslands, once already ploughed in the past, protect potential arable land if there arise a necessity of increased food production in the future.

Importance for landscape planning and management of protected areas

In my opinion, distinguishing between ancient and recent grasslands will be beneficial for different landscape planning projects or for better targeting of agricultural policy. One example is the identification and assessment of High Nature Value farmland (Peppiette et al. 2012, Stenzel et al. 2017).

If for some reason there is doubt about the historical status of a particular grassland (e.g. insufficient documentation on old maps), the indicator species may be used retrospectively to determine whether it is rather an ancient or recent grassland.

Distinguishing between ancient and recent grasslands should be applied in the management of protected areas. Ancient grasslands should be strictly protected against loss of area and large disturbances. On the other hand, recent grasslands should be subjected to more intense disturbances, and possibly even tilled, in order to retain particular successional stages or to regenerate the seed banks of rare weeds or low-competitive species (chapter 4).

Summary of the importance for the nature conservation and restoration practice

Both ancient and recent grasslands in the study regions are more or less well preserved. The vegetation of ancient grasslands seem to be generally more valuable from a conservation point of view. Although less species of endangered plants occur in recent grasslands, they are a special part of a flora that does not grow in many other habitats. The situation regarding the soil seed banks is different. Soil seed banks of ancient grasslands have only a low significance for the maintenance or restoration of biological diversity of dry grasslands. However, the soil seed banks of recent grasslands can store seeds of rare species favoring disturbances, such as arable weeds, which otherwise do not occur in current grasslands and fields.

Thus, our results concerning the conservation value of ancient and recent grasslands are neither unambiguous nor trivial. However, the grasslands included in the dissertation are quite well preserved. In common Central European landscapes, where in less favoured regions huge areas of arable land were abandoned and converted to grasslands over in the last decades, we can expect overall much bigger differences between ancient and recent grasslands. Therefore, the importance of ancient grasslands can be expected to be more pronounced in more common landscapes with lower conservation status.

Summary

Dry calcareous grasslands are among the most species-rich habitats in Central Europe, harbouring numerous threatened species. In the majority of the area, the grasslands are semi-natural, but with high biodiversity and the presence of relict plant species. This is why it is the focus of scientific research and, consequently, of nature conservation.

Spatial dynamics of this habitat is not trivial and unidirectional, because in addition to strong decline, many new areas have also emerged on abandoned arable fields. Therefore, two concepts, ancient and recent grasslands, have been defined in order to better approach the researched issue.

The present dissertation aims at understanding of effect of age on quality of particular grasslands. The main approach was the phytosociological sampling of above-ground vegetation, attention was also paid to the soil seed bank. Additionally, wide range of abiotic parameters were measured.

The study was carried out in three regions with well-preserved dry grassland vegetation: Swabian Alb in Baden-Württemberg (Kaltes Feld), Franconian Alb in Bayern (Kallmünz) and Bohemian Karst in Bohemia (Srbsko) (Fig. 1.8).

Chapter 2 deals with vegetation of ancient and recent grasslands in **Kaltes Feld** region in Swabian Alb in the South of Germany.

I identified plant species indicating the historical status of the grasslands. Indicators for ancient grassland are assigned mainly to phytosociological class *Festuco-Brometea* (e.g. *Carex flacca, Carlina vulgaris, Cirsium acaule, Hippocrepis comosa*). Indicators for recent grasslands are phytosociologicaly more heterogenous and includes besides of some dry-grasslands species a lot of species from mesophilous meadows, thermophilous edges and arable weeds (*Rhinanthus alectorolophus*) or even former crops (*Onobrychis viciifolia*). I found a lot of rare and/or endangered species not only in ancient but in recent grasslands as well. Furthermore, recent grasslands show high species diversity. If they are well-preserved, then both, ancient and recent calcareous grasslands should be equally valued from nature-conservation point of view.

I found significant differences in some abiotic habitat parameters, especially in soil reaction and water-holding capacity. The history (former land-use, age of habitats) of grassland localities is a fundamental attribute which very good explains species composition of vegetation and is not simply replaceable by habitat properties. Therefore, I can state that both history and habitat properties are responsible for the actual species composition pattern.

Also in **chapter 3** was the main question which species may indicate the age of a dry calcareous grassland habitat. This time was the study conducted in another part of the south Germany, in the Franconian jurassic mountains near small town Kallmünz. Furthermore, I asked if there is a general pattern of indicator species among available studies on ancient and recent calcareous grasslands. I compared the diversity parameters and nature conservation value of both grassland types. I searched also for differences in habitat and soil parameters.

I compiled not only a list of indicator species of both ancient and recent grasslands in the study region but I made a search of other studies and prepared review table. From this table is obvious that

there are not many species that clearly indicate grassland age across different regions (the best indicators are *Carex caryophyllea*, *Cirsium acaule* and *Hippocrepis commosa* for ancient grasslands, and *Agrimonia eupatoria* and *Astragalus glyciplyllos* for recent grasslands).

Ancient grasslands in Kallmünz harbour a somewhat greater number of threatened species than recent grasslands. However, also recent grasslands harbour rare and endangered species, especially disturbance-tolerant relicts of former arable use (e.g. *Melampyrum arvense*) and may therefore have high conservation value, too. The average number of species per plot is greater in ancient grasslands. However, the most species-rich plot (46 species of vascular plants within a 4-m2 quadrat) was found in a 60 years old recent grassland.

Arable cultivation in the past has altered the physical and chemical properties of the soil of recent grasslands. In general, ancient grasslands occur on nutrient-poorer and less calcareous-rich soils with high water-holding capacity. High water-holding capacity is connected with high humus content, which increases the importance of ancient grasslands for carbon storage.

In **chapter 4** I focused on soil seed banks of calcareous grasslands. Soil seed banks are important because they represent specific „vegetation archive“ and can be potentionaly important for restoratition of previous species diversity on degraded plots. I compared soil seed banks and aboveground vegetation of recent and ancient calcareous grasslands in the two regions of Southern Germany which were subjected to the vegetation analyses already described in chapter 2 a 3: the western Jurassic mountains (Kaltes Feld) and the climatically drier eastern part of Southern Germany (Kallmünz).

Total number of species in the seed bank was similar in both regions, but species composition partly differed, reflecting phytogeographical differences between the regions. The total number of emerged seedlings showed a large disparity (5457 compared to 2523 seedlings/m2 in Kaltes Feld and Kallmünz, respectively).

Though there were differences in seed bank composition and size, we found a uniform pattern of plant traits (affiliation to phytosociological groups, Raunkiaer plant life-forms and seed longevity), which depended on the age of the grassland. The main conclusion is that seed banks in contemporary calcareous grasslands still reflect the history of former land use, in this case arable cultivation, even though it occurred a long time ago (up to 150 years). Indicators of former arable fields are germinable seeds of weeds which have persisted in the soil to the present. By contrast, weedy species are completely absent from the seed banks of ancient grasslands. My research has confirmed the findings of other authors that soil seed banks of dry grasslands are not a good tool for their restoration (e.g. recovery of typical dry drassland species). However, soil seed banks of recent grasslands may store seeds of rare and endangered weed species (e.g. *Kickxia spuria*, *Silene noctiflora* and *Stachys annua*) and thus be of conservation importance because it allows the recovery of these species.

Chapter 5 also deals with soil seed banks. It is only small case study, but represent the first contribution to knowledge about the soil seed banks of ancient grasslands in the Český kras/Bohemian Karst, very famous and conservationaly valuable dry grassland region. The studied site belongs to the alliance *Cirsio-Brachypodion* with strong dominance of *Bromus erectus,* probably an alien species in the Český kras/Bohemian Karst, which suppresses the species diversity of aboveground vegetation.

Nevertheless, some rare species such as *Aster amellus*, *Helianthemum canum*, *Pulsatilla pratensis* and *Stachys germanica* were found there. The soil seed bank is very low in the both species and seedling numbers. The absence of weeds and species of young grasslands in the soil seed banks confirms that the site was not used as an arable field in the past. The presence of germinable seeds of *Potentilla incana*, *Linum catharticum*, *Sedum acre* and *S. sexangulare* indicates that the grassland studied was once richer in species due to grazing-induced disturbances in the past.

Chapter 6 summarizes perspectives of using knowledge about the history of grasslands in the nature conservation and restoration practice.

Both ancient and recent grasslands can be very well preserved and highly valuable from a nature protection point of view. The species diversity seems to be generally higher in ancient grasslands, but some recent grasslands are also extremely species-rich. More endangered species occur in ancient grasslands, but many rare species are also typical of recent grasslands, some of them even as an exclusive species. But some species are too sparse to be captured by surveying using randomly placed phytosociological samples. Therefore, another, more extensive approach as floristic mapping is appropriate, what was documented on gentian species.

Soil seed banks of dry grasslands have only low importance for habitat restoration. However, this is only true for ancient grassland indicators. In contrast to ancient grasslands, the soil seed bank of recent grasslands may have a high importance for the conservation of rare weeds.

Thus, results concerning the conservation value from a species diversity point of view are neither unambiguous nor trivial, since they contradict other studies which point out a higher value of ancient grasslands.

I am convinced that distinguishing between ancient and recent grasslands will be useful in the management of protected areas. Ancient grasslands should be strictly protected against loss of area and large disturbances. On the other hand, recent grasslands should be subjected to more intense disturbances, and possibly even tilled, in order to retain particular successional stages or to regenerate the seed banks of rare weeds or low-competitive species.

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